Historical knowledge, variation in community composition, ecotrophic parameterization, and invasive species of macroalgae in the Galapagos archipelago

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Historical knowledge, variation in community composition, ecotrophic parameterization, and invasive species of macroalgae in the Galapagos archipelago

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Abstract

Due to its uniqueness and protected status the marine ecosystem of the Galapagos Marine Reserve (GMR) is of particular interest. As a result of its equatorial location and upwelling-influenced waters, the Galapagos archipelago hosts a diverse and productive marine ecosystem, and this is especially true of marine macroalgae. Macroalgal ecology in the archipelago has not been comprehensively studied, and Chapter 1 is a compilation and discussion of relevant literature-an attempt to summarize and integrate the available knowledge so that important gaps may be identified as foci for for future research.

Over 300 species of macroalgae have been described in the Galapagos, and grazers (including marine reptiles, fish, and invertebrates) represent a large portion of the nearshore marine food web. There is anecdotal evidence of variability in macroalgal diversity and abundance across the islands, with the north being described as "barren," the "Central/South" as "patchy" and the West as "diverse and abundant." These differences could have an important influence on the structure of energy flows through shallow ecosystems. Previous work has highlighted the critical role of macroalgal productivity and dynamics in supporting and structuring marine food webs in the Galapagos archipelago, and estimates of benthic primary productivity (macroalgae) vary regionally, though the basis of this variation has not been accounted for.

Chapter 2 describes the variation in functional group compositions of macroalgal communities across the archipelago (surveys of 50 transects at 30 sites), and confirms the three-region scheme described previously. Macroalgal communities in the Galapagos are generally dominated by the 'Calcareous Crustose' functional group, though variation in the cover of 'Filamentous' and 'Thin Foliose' groups is important in determining overall dissimilarity between transects. These latter two groups are highly productive compared to the first, and results showed significantly higher cover of the 'Thin Foliose' group in shallower water.

In Chapter 3 these community compositions were used to estimate biomass and production parameters for all macroalgal communities surveyed. These parameters were compared across sites and depths and with the results of published sub-system models. MaC biomass was threefold higher in the West than in the North or South/Central. MaC production was higher in the West than the Central/South, but did not vary otherwise. Production/Biomass ratios, while generally lower in the West, did not vary significantly across regions. Overall, cover of the 'Filamentous' group had the most positive influence on P/B per transect. Mean MaC production was higher in 6m than in 15m, and an exclusion experiment showed MaC production in the absence of herbivores to be greater in 6m than in 15m. ENSO-driven changes in macroalgal communities have been implicated in precipitous declines in grazer populations, highlighting the potential importance of bottom-up control in the system. As the survey period of this work coincided with "ENSO-neutral" conditions, the information presented here can serve as a baseline for quantifying macroalgal dynamics across ENSO cycles.

Chapter 4 presents the results of a collaborative research project with the Charles Darwin Foundation's marine invasive species project, whose goal it was to understand the history, phylogeny, and potential ecological impacts of the green alga *Caulerpa* in the Galapagos Marine Reserve. First recorded in 1899, *Caulerpa* has been reported from both intertidal and subtidal habitats across the archipelago, and was recently reported as increasing in abundance on coral reefs at Darwin Island. The majority of historical reports, and all genetic samples processed to date, correspond to *C. chemnitzia* and *C. racemosa,* pantropical entities which belong to a polyphyletic complex *Caulerpa* species. Cover of *Caulerpa* was not recorded in 2012 at Darwin's Arch, but by 2014 had reached 15%, exceeding that of live coral. We recommend expanded and continued monitoring of the distribution and phylogenetics of *Caulerpa* in the GMR, and stress vigilance across stakeholder groups in order to identify any potential future changes in its behavior.

Overall this body of work presents important findings, and contributes to our knowledge of macroalgal ecology in the Galapagos archipelago. This work, which included a synthesis of historical knowledge, a large-scale description of macroalgal community variation across the archipelago based on standardized surveys, large and fine-scale estimates of macroalgal ecotrophic parameters, and the foundation for studying the phylogenetics and behavior of *Caulerpa* in the GMR, was completed with the hope that this information will be useful for the continued management and conservation of the unique and fragile marine ecosystems of the Galapagos archipelago.

Keywords: Galapagos, macroalgae, trophic models, historical ecology, *Caulerpa*

Resumen

Debido a su especial singularidad y estatus de protección, el ecosistema marino de la Reserva Marina de Galápagos (GMR) es de particular interés. Como resultado de su ubicación ecuatorial y las aguas influenciadas por afloramiento, el archipiélago de Galápagos alberga un ecosistema marino diverso y productivo, especialmente para las macroalgas marinas. La ecología de las macroalgas en el archipiélago no se ha estudiado de manera exhaustiva y el Capítulo 1 presenta una recopilación y discusión sobre literatura relevante y un intento de resumir e integrar el conocimiento disponibles para identificar las brechas importantes como puntos focales para futuras investigaciones.

Más de 300 especies de macroalgas han sido descritas en Galápagos, y los pastoreadores (incluyendo reptiles marinos, peces e invertebrados) representan una gran proporción en la red trófica marino costera. Existe evidencia anécdotal sobre la variabilidad en la diversidad y abundancia de macroalgas en las islas, siendo el norte descrito como "estéril", el "Central/Sur" como "irregular" y Occidente como "diverso y abundante". Estas diferencias pueden tener una gran influencia en la estructura de los flujos de energía a través de ecosistemas poco profundos. Trabajos previos han destacado el papel crítico de la productividad y dinámica de macroalgas en el apoyo y la estructuración de las redes alimenticias marinas en el archipiélago de Galápagos. Las estimaciones de la productividad primaria béntica (macroalgas) varían regionalmente, aunque la base de esta variación no se ha tenido en cuenta.

El capítulo 2 describe la variación en la composición de los grupos funcionales de la comunidades de macroalgas atreves de todo el archipiélago (monitoreos de 50 transectos en 30 sitios) y confirma el esquema de las tres regiones descrita anteriormente. Las comunidades de macroalgas de las Galápagos están generalmente dominadas por el grupo funcional "Calcáreas Crustosas", aunque la variación en la cobertura de los grupos "Filamentosas" y "Foliosas Delgadas" es importante para determinar la disimilitud general entre los transectos. Estos dos últimos grupos son altamente productivos en comparación con el primero, y los resultados muestran una cobertura significativamente mayor del grupo de "Foliosas Delgadas " en aguas menos profundas.

En el Capítulo 3, estas composiciones comunitarias se utilizaron para estimar biomasa y parámetros de producción para todas las comunidades de macroalgas estudiadas. Estos parámetros se compararon entre sitios y profundidades, y con los resultados de modelos de subsistemas publicados. La biomasa MaC fue tres veces mayor en Occidente que en el Norte o Sur/Central. La producción de MaC fue más alta en Occidente que en el Centro/Sur, pero no varió de otra manera. La relación producción/biomasa, aunque generalmente más bajas en Occidente, no variaron significativamente entre las regiones. En general, la cobertura del grupo 'Filamentosas' tuvo la mayor influencia positiva en P/B por transecto. La producción media de MaC fue mayor en 6m que en 15m, y un experimento de exclusión mostró que la producción de MaC en ausencia de herbívoros era mayor en 6m que en 15m. Los cambios impulsados por el ENSO en las comunidades de macroalgas han estado implicados en descensos abruptos en las poblaciones de pastoreadores, destacando la importancia potencial del control ascendente en el sistema. Como el período del muestreo de este trabajo coincidió con condiciones "ENSO-neutral", la información presentada en este trabajo puede servir

como línea base para cuantificar la dinámica de las macroalgas a través de los ciclos ENSO.

El capítulo 4 presenta los resultados de una investigación colaborativa con el proyecto de especies marinas invasoras de la Fundación Charles Darwin, cuyo objetivo es comprender la historia, la filogenia y los posibles impactos ecológicos de la alga verde *Caulerpa* en la Reserva Marina de Galápagos. Esta alga se registró por primera vez en 1899, *Caulerpa* se ha registrado en los hábitats intermariales y submareales a través del archipiélago, y se ha propagado recientemente, con un aumento en abundancia en los arrecifes coralinos en la isla de Darwin. La mayoría de los informes históricos, y todas las muestras genéticas procesadas hasta la fecha, corresponden a *C. chemnitzia* y *C. racemosa*, entidades pantropicales que pertenecen a una especie polifilética del complejo *Caulerpa*. La covertura de *Caulerpa* no fue registrada en 2012 en el Arco de Darwin, pero para 2014 había alcanzado el 15%, superando la de los corales vivos. Este trabajo recomendienda un monitoreo extensivo y continuo para entender la distribución y filogenética de *Caulerpa* en el GMR, además de la vigilancia sobre el estrés entre los grupos de interés con el fin de identificar posibles cambios en su comportamiento a futuro.

En conjunto, este trabajo presenta hallazgos importantes y contribuye a nuestro conocimiento sobre la ecología macroalga en el archipiélago de Galápagos. Este trabajo, que incluyó una síntesis del conocimiento histórico, una descripción a gran escala de la variación de la comunidad de macroalgas en todo el archipiélago a partir de muestreos estandarizados, estimaciones detallas sobre los parámetros ecotróficos de macroalgas y la base para estudiar la filogenética y el comportamiento de *Caulerpa* en el RMG, se completó con la esperanza de que esta información sea útil para el manejo continuo y la conservación de los ecosistemas marinos únicos y frágiles del archipiélago de Galápagos.

Palabras claves: Galapagos, macroalgas, modelos tróficos, ecología histórica, *Caulerpa*

Zusammenfassung

Aufgrund seiner Einzigartigkeit und den besonderen Schutzstatus ist das marine Ökosystem des Galapagos Marinen Reservats (GMR) von speziellem Interesse. Als Folge des äquatornahen Standortes und des auftriebsbeeinflussten Wassers beheimatet das Galapagos Archipel ein diverses und produktives marines Ökosystem, was sich besonders in den marinen Makroalgen widerspiegelt. Die Ökologie der Makroalgen des Archipels wurde bisher nicht umfassend untersucht, und so ist Kapitel 1 eine Zusammenstellung und Diskussion entsprechender Literatur – der Versuch, das verfügbare Wissen zusammenfassend zu integrieren, um wichtige Lücken als Foki zukünftiger Forschung zu identifieren.

Über 300 Makroalgenarten wurden für das Galapagos Archipel beschrieben, und Herbivore (einschließlich mariner Reptilien, Fische und Invertebraten) repräsentieren einen großen Bestandteil des küstennahen marinen Nahrungsnetzes. Es liegt anekdotenhafter Beweis bezüglich der Variabilität von Makroalgenbiodiversität und -abundanzen auf den Inseln vor, wobei der Norden als „unfruchtbar", die Mitte-Süd als „fleckig" und der Westen als „divers und abundant" beschrieben wird. Diese Unterschiede könnten einen wichtigen Einfluss auf die Struktur der Energieflüsse in seichten Ökosystemen haben. Vorausgehende Arbeiten haben die entscheidende Rolle von Makroalgenproduktivität und –dynamiken für die Struktur mariner Nahrungsnetze des Galapagos Archipels hervorgehoben, und außerdem dargestellt, dass die benthische Primärproduktion (Makroalgen) regional variabel ist, obwohl die Ursache für diese Schwankungen noch nicht bekannt ist.

Kapitel 2 beschreibt die Veränderung der Zusammensetzung funktioneller Gruppen von Makroalgengemeinschaften im Archipel (Erhebungen von 50 Transekten an 30 Standorten) und bestätigt das oben beschriebene Drei-Zonen Schema. Makroalgengemeinschaften in Galapagos sind generell dominiert von der funktionellen Gruppe der„kalkhaltigen Krustenalgen", obwohl die Schwankungen in der Bedeckung von „Fadenalgen" und „dünne Blattalgen" für die Erklärung der Unterschiede zwischen den Transekten wichtig sind. Die beiden letzten Gruppen sind im Vergleich zu der ersten höchst produktiv und die Ergebnisse zeigen eine signifikant höhere Bedeckung durch „dünne Blattalgen" in seichterem Wasser.

In Kapitel 3 wurden diese Zusammensetzungen dafür verwendet, Biomasse- und Produktivitätsparameter für alle Makroalgengemeinschaften zu untersuchen. Diese Parameter waren vergleichbar mit den Ergebnissen bisher veröffentlichter Modelle für Teilsysteme des Archipels. MaC Biomasse waren im Westen dreimal so hoch wie in der Mitte-Süd, aber unterschieden sich ansonsten nicht. Die Produktion/Biomasse-Verhältnisse, obwohl generell niedriger im Westen, unterschied sich nicht signifikant in den Regionen. Insgesamt hatte die Bedeckung von „Fadenalgen" den positivsten Effekt auf P/B pro Transekt. Durchschnittliche MaC Produktion war höher in 6m als in 15m

Wassertiefe, und ein Auschlussexperiment resultierte in 6m Wasertiefe in einer höheren MaC Produktion in Abwesenheit von Herbivoren, als in 15m. ENSO-getriebene Veränderungen in Makroalgengemeinschaften wurden bisher für drastische Rückgänge von Herbivorpopulationen verantwortlich gemacht, was die potenzielle Wichtigkeit von Bottom-Up-Kontrollen innerhalb des Systems hervorhebt. Da der Studienzeitraum der vorliegenden Arbeit unter „ENSO-neutralen“ Bedingungen stattfand, könnten die hier vorgestellten Informationen als Grundlinie für die Quantifizierung der Dynamiken von Makroalgen über ENSO-Zyklen dienen.

Kapitel 4 stellt die Ergebnisse einer gemeinschaftlichen Arbeit mit dem Projekt zu invasiven marinen Arten der Charles Darwin Foundation vor, dessen Ziel es war, die Geschichte, Phylogenie und mögliche ökologische Auswirkungen der Grünalge Caulerpa im Galapagos Marinen Reservat zu verstehen. Seit ihrer ersten Erfassung in 1899 wurde Caulerpa sowohl in intertidalen und als auch in subtidalen Habitaten des gesamten Archipels gesichtet und wurde zuletzt mit erhöhter Häufigkeit auf Korallenriffen der Insel Darwin gemeldet. Die Mehrheit der historischen Berichte und alle bisher ausgewerteten genetischen Proben entsprechen C. chemnitzia und C. racemosa, pantropische Einheiten einer phylophyletisch komplexen Caulerpa Art. Am Standort Darwin’s Arch wurde Caulerpa im Jahr 2012 nicht dokumentiert, allerdings hatte die Bedeckung durch die Alge bis 2014 bereits 15% erreicht, und damit die Bedeckung durch lebende Korallen überstiegen. Wir empfehlen eine großflächige und kontinuierliche Überwachung der Verteilung und Phylogenie von Caulerpa im GMR und betonen die Wachsamkeit der verschiedenen Nutzergruppen um weitere mögliche zukünftige Veränderungen in der Verbeitung zu beobachten.

Insgesamt legt diese Arbeit wichtige Ergebnisse vor, und trägt zu unserem Wissen über die Ökologie der Makroalgen im Galapagos Archipel bei. Diese Arbeit, die eine Synthese historischen Wissens, eine umfassende Beschreibung der Veränderungen in der Makroalgengemeinschaften des Archipels, eine groß- und kleinskalierte Bestimmung von ökotrophischen Parametern der Makroalgen sowie die Grundlage für die Untersuchung der Phyolegenie und des Verhaltens von Caulerpa im GMR umfasst, wurde mit der Hoffnung verfasst, dass die Information nützlich sein möge für das fortführende Management und den Erhalt dieses einzigartigen und fragilen marinen Ökosystems des Galapagos Archipels.

Schlüsselwöter: Galapagos, Makroalgen, trophische Modellierung, historische Ökologie, *Caulerpa*

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General Introduction

This work was primarily completed to meet the goals of the COGA (Functional role of Carbonate secreting Organisms in upwelling and non-upwelling zones of the Galápagos marine ecosystem) project, a collaborative research venture between Dr. Hildegard Westphal, Prof. Dr. Matthias Wolff, Dr. Claire Reymond, Dr. Diego Ruiz, and Dr. Jochen Halfar. Other collaborators in this work include Dr. Stuart Banks, Dr. Fernando Rivera, Dr. Bernard Kegel, and Dr. Inti Keith. Fieldwork for the project was conducted within the Galapagos Marine Reserve, which is administered by the Galapagos National Park, and permitted under the title: "Registros de acidificación y frentes oceánicos en organismos de carbonato de calcio en las islas Galápagos", and included in the "POA 2012" of the Charles Darwin Foundation (CDF) under the project: S7 *"Investigación en la ecología de especies marinas prioritarias para la conservación (especies recursos y especies enfoque)."*

In 1986, the Galapagos Marine Reserve (GMR) was created. A management plan signed into law in 1992 allowed for local-scale, artisanal fisheries, while severely limiting industrial-scale marine resource extraction (Camhi 1995). In 1998 a new law signed by the President of Ecuador expanded the GMR to reach 40 nautical miles from the coastlines of all islands to cover a sea surface area of 133,000km^2, and completely banned all industrial fisheries. Since the implementation of this special law, the GMR has been managed by a participatory management board whose members include representatives from fishing, nature guiding, tourism, research/conservation, and administration sectors (Toral-Granda 2005).

Though situated at the equator where ocean water is normally uniformly warm, the Galapagos Archipelago's location at the confluence of warm and cold ocean currents, combined with consistent upwelling of cold waters at the archipelago's western margin, causes the waters surrounding the islands to experience a range of temperatures and nutrient-enriched productivities. As a result, the Galapagos hosts a fantastic mixture of marine species normally only found in either tropical or cold-temperate environments. Tourism, fishing, research, and conservation interests all hinge on the biodiversity and productivity of the waters around the islands, which are greatly influenced by oceanographic cycles. Strong ENSO (El Nino Southern Oscillation) events have had particularly deleterious and highly visible effects on marine life (Robinson & del Pino, 1985).

Relatively recent (1982/83, 1997/98) and powerful ENSO events have resulted in species extinctions and fundamental changes in energy flows through the marine trophic web of the Galapagos (Edgar et al., 2010). Successful management of fisheries requires understanding the coupling between environmental change and ecological dynamics, and recent research efforts have focused on modeling energy flows through the marine food web, so that these dynamics may be predicted and accounted for in management

schemes. Given its protected status, multiple stakeholder interests, and oceanographically driven productivity, understanding the trophic structure and function of the marine ecosystem is of particular importance.

Planktonic and benthic primary production form the foundation of the Galapagos marine ecosystem, upon which all higher trophic levels depend. Macroalgae (algae easily visible to the human eye, or seaweeds) have historically reported as locally abundant in the archipelago, as have herbivorous fish, reptiles, and invertebrates that consume macroalgae. While various taxonomic ventures in the Galapagos have produced diversity estimates of well over 300 macroalgal species, no large-scale ecological information exists for the region. Rather, information is available from disparate sources, and often as anecdotes or field notes. Therefore, Chapter 1 presents a review of available ecological information about Galapagos macroalgae as of August of 2016, when the manuscript was accepted for publication in *Revista de Biologia Tropical* (Tompkins & Wolff, 2017). In this chapter, a regionalization scheme of macroalgal community abundance and composition is presented based on reviewed literature.

This information provided the basis for a large-scale macroalgal community survey across the Galapagos archipelago, and Chapter 2 presents the results of this work. In this chapter, a functional group approach is developed for classifying Galapagos macroalgal species according to their gross morphologies. PCA analyses were used to determine which functional groups are most influential in determining dissimilarity between survey locations, and Cluster analyses were used to determine the number and identity of groups within the data. The results show variation in the cover, identity, and number of functional groups present across the archipelago, and across the two depth strata surveyed (6 and 15 meters).

The functional groups developed in Chapter 2 vary greatly in their morphologies and productivity potential. Grazers are an important part of the marine ecosystem in the Galapagos, and spatio-temporal variability in macroalgal biomass and productivity across the archipelago could have an important role in structuring marine communities and influencing energy flows through the food web. Small-scale trophic models have been created in the archipelago to characterize the energy flow structure of the Galapagos marine ecosystem and to allow for predictions of changes in system configuration and energy flow pathways in response to fluctuating physical and biological variables (Okey et al., 2004; Ruiz & Wolff, 2011). These models were created for limited areas, and exhibit large disparities in estimates of standing stocks of benthic primary producers (macroalgae).

Integration of larger scale knowledge of ecological patterns and processes is necessary to improve predictive power across the spatial extent of the GMR. Chapter 3 therefore presents biomass and production values for all areas surveyed in Chapter 2, in order to more accurately parameterize larger-scale ecotrophic models and provide a baseline for ENSO-driven changes. Overall higher production was estimated for

shallower transects, and results of a macroherbivore (fish and urchin) exclusion experiment suggest that depth-related differences in production are not influenced by macroherbivore herbivory, at least during ENSO-neutral conditions.

Chapter 4 presents the results of a collaborative project between the author, CDF researcher Dr. Init Keith, and Dr. Thomas Sauvage of the University of Louisiana at Lafayette. Human impacts have threatened many of the unique and iconic species in Galapagos. Introductions of alien invasive species such as rats, pigs, and flies have devastated populations of Galapagos iguanas, tortoises, and finches. Documented introductions of crabs and hydroids have highlighted the potential for marine alien species to gain a foothold in the GMR, and alien macroalgal introductions and invasions are a looming threat (Keith, 2016). Seaweeds in the genus *Caulerpa* are known to be aggressive alien invaders in tropical and warm-temperate waters worldwide, and can smother and kill corals (Schaffelke et al., 2006; Klein & Verlaque, 2008). *Caulerpa* was first reported in Galapagos over a century ago, and recent reports of *Caulerpa* blooms on an iconic coral reef at Darwin Island prompted the CDF to prioritize research into the ecological history and systematics of *Caulerpa* in the GMR. Chapter 4 is a synthesis of a recent research effort on this subject, and has been submitted for peer review to *Frontiers in Ecology and Evolution*.

Finally, all of these results are synthesized in a general discussion. Larger-scale implications of the work are presented, in order to view the findings in a broader context. Lastly, this body of work is used as a foundation for future avenues of marine ecological research across broad time and spatial scales. In particular, focus should be on continued long-term and large-scale monitoring, analysis of available historical datasets, and mechanistic studies to elucidate the factors driving macroalgal patterns and dynamics.

Formatting: Chapter 1 has been published in *Revitsa de Biologia Tropical* (Tompkins & Wolff, 2017), and therefore follows the formatting requirements of the journal. For clarity and continuity, the balance of this dissertation is presented in a similar format, including Chapter 4, which has been submitted for review to *Frontiers in Ecology and Evolution* (Tompkins, Keith, and Sauvage).

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Chapter 1: Galapagos macroalgae: A review of the state of ecological knowledge

Abstract: Previous work has highlighted the critical role of macroalgal productivity and dynamics in supporting and structuring marine food webs. Spatio-temporal variability in macroalgae can alter coastal ecosystems, a relationship particularly visible along upwelling-influenced coastlines. As a result of its equatorial location and nutrient rich, upwelling-influenced waters, the Galápagos Archipelago in the Tropical East Pacific hosts a productive and biodiverse marine ecosystem. Reports and collections of macroalgae date back to the *Beagle* voyage, and since then, more than three hundred species have been reported. However, the ecology and functional role of macroalge in the ecosystem is not well understood. According to various disparate and in part anecdotal sources of information, abundant and diverse communities exist in the Western regions of the archipelago, the North is essentially barren, and in the South/Central region macroalgal abundance and distribution is variable and less well defined. Both oceanographic conditions and herbivore influence have been theorized to cause this pattern. Extensive changes in macroalgal productivity and community composition have occurred during strong ENSO events, and subsequent declines in marine iguana (an endemic and iconic grazer) populations have been linked to these changes. Iguanas are only one species of a diverse and abundant group of marine grazers in the system, highlighting the potentially important role of macroalgal productivity in the marine food web. This review represents a first compilation and discussion of the available literature and presents topics for future research.

Keywords: Macroalgae, Galapagos, historical ecology, marine herbivores, marine ecology

INTRODUCTION

Marine macroalgae, or seaweeds as they are commonly known, are an important source of marine primary productivity, and provide a range of ecosystem services (Mann, 1973; Dayton, 1985). Macroalgal morphologies range from tiny simple filaments and crustose forms which creep along the seafloor and grow less than a millimeter a year to massive, towering species like the kelp *Macrocystis* which can grow half a meter a day and attain frond lengths of over 30 meters (Lobban & Harrison, 1997). The species richness of kelp-associated benthic communities (specifically forests of *Macrocystis*) rivals that of the most biodiverse habitats on the planet (Dayton, 1985), and degradation or loss of macroalgal habitat results in fundamental changes in benthic community structure, and declines in functional diversity and overall productivity (Bodkin, 1988; Graham, 2004; Lilley & Schiel, 2006).

Macroalgal distributions are spatiotemporally variable due to a variety of factors including oceanography, disturbance, and herbivory (e.g. Kerswell, 2006; Santelices, Bolton, & Meneses, 2009). Upwelling regions, and in particular island archipelagos within those regions, exhibit variable macroalgal distribution patterns across ranges of upwelling influences, making them ideal locations for the study of macroalgal biogeography and dynamics (Bustamante & Branch, 1996; de Guimaraens & Coutinho, 1996; Schils & Coppejans, 2003b). While macroalgal ecology in other upwelling influenced island systems (e.g. Canary Islands, Arabian Sea, California Current) has been well studied, the Galápagos archipelago is a notable exception.

Because of its relative remoteness, oceanographic complexity, biological diversity, and high proportion of endemism, the Galápagos archipelago presents a 'living laboratory' for ecological and evolutionary investigations. Taxonomy and biogeography are particularly fruitful fields of investigation, and geographic affinities of marine mammals, birds, fish, and macroinvertebrate species have already been described (Harris, 1969; Grehan, 2001; Palacios, 2003; Edgar et al., 2004). Oceanographic and meteorological processes combine in the equatorial East Pacific to create large spatiotemporal gradients in surface water temperatures across the Galápagos Islands (Palacios, 2004), and upwelled nutrient-rich waters create rich phytoplankton blooms twice as dense as in surrounding waters, supporting a highly productive marine ecosystem (Palacios, 2004; Pennington et al., 2006; Ruiz & Wolff, 2011).

Macroalgae exist in the archipelago, and the most exhaustive (and available) investigations of Galápagos macroalgae have been taxonomic in nature (reviewed by Garske, 2002).

Current estimates of marine macroalgal richness are upwards of 315 species, containing taxa representative of tropical and temperate waters. Ecological information includes anecdotal or coincidental observations of ecological patterns and processes,

ecological models of shallow subtidal systems, and manipulative experiments designed to test top-down and bottom-up influences on the marine flora of the archipelago. This review offers a compilation and discussion of relevant literature-an attempt to summarize and integrate available knowledge-so that gaps in understanding of Galápagos macroalgal ecology may be identified as areas for future research. Three main themes include: 1) distributions (influences of oceanography, depth, and herbivores), 2) temporal dynamics (primarily the influence of El Niño Southern Oscillation-ENSO), and 3) functional role (grazer diversity and abundances, ecosystem services).

Material for this review was gathered from several sources, including the physical holdings of the Charles Darwin Foundation (CDF) Library, online information in the CDF's Datazone, and notations and samples from the collections at the CDF and University of California Berkeley Herbariums. Online searches for relevant literature, combined with institutional requests for specific materials, formed the balance of the review effort. Material reviewed dates from the earliest records available (1800's), to present day.

DISTRIBUTIONS

Regional variation:

Via deleterious effects on physiology and competitive interactions, thermal stresses and nutrient limitations can limit macroalgal distributions (Adey & Steneck, 2001). Global trends exhibit a propensity for diverse and abundant macroalgal communities to flourish in relatively cold, nutrient rich waters (higher latitudes), while entirely different and relatively species-poor assemblages of species inhabit warm and generally nutrient-limited tropical waters (Schils & Coppejans, 2003a; Kerswell, 2006). This general pattern is confounded by smaller-scale physical and biological factors, such as tropical upwelling, anthropogenic nutrient pulses, and localized overabundances of grazers (Bell, 1992; Lobban & Harrison, 1997). Work in other upwelling influenced areas has revealed oceanographic and herbivore related biogeographic patterns in macroalgal community compositions and biomasses, with diversity and abundances related positively to upwelling (colder, nutrient rich waters) influence, and negatively to grazer (urchin) abundances (Bustamante & Branch, 1996; Schils & Coppejans, 2003a; Sangil, Sansón, & Afonso-Carrillo, 2011).

In Galápagos, consistent upwelling of cold waters at the archipelago's Western margin and seasonally alternating warm (surface waters from the Northeast) and cold (upwelled waters from the Southeast) currents cause the waters surrounding the islands to experience a range of temperatures and productivities over time. At the peak of upwelling, sea surface temperatures across the archipelago can differ by more than 10 °C.

Previous work has identified distinct regions within the archipelago, based on

both physical characteristics and organismal distributions (e.g. Harris, 1969). Edgar et al. (2004), for example, divided the archipelago into five main regions, based on biogeographic patterns of marine fish and macroinvertebrates. Patterns and trends in the distribution of Galápagos macroalgae have been noted by several investigators, and both physical (temperature, nutrients, depth) and biological (herbivory) influences have been postulated (e.g. Wellington, 1984). Important biogeographic insights from both taxonomic and ecological studies are here presented, and offer a promising platform for further research. Overall, outstanding trends noted by investigators divides the archipelago into 1) Western, 2) Northern, and 3) South/Central regions based on the diversity and abundance of macroalgal communities. For reference, these regions are depicted in figure 1.

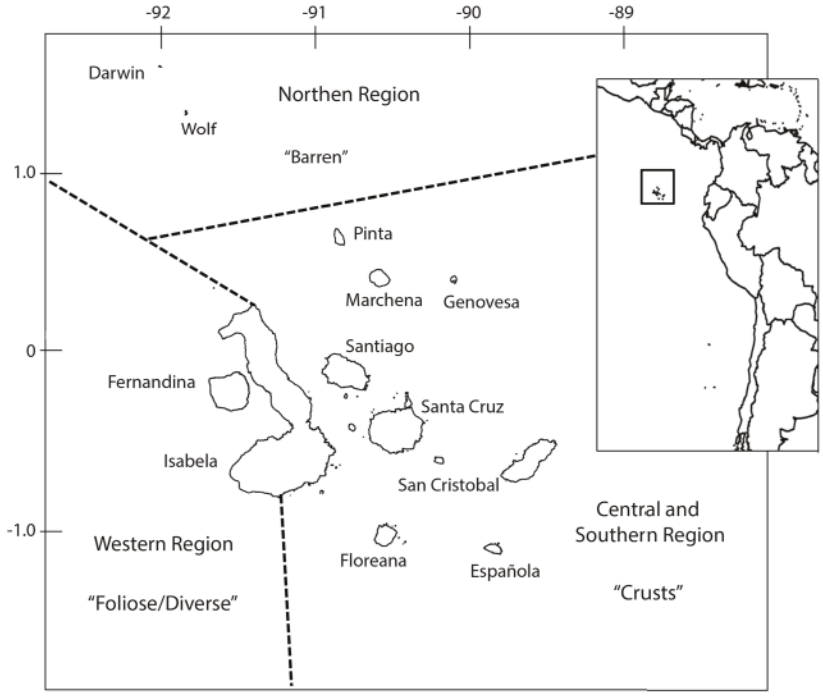

Figure 1. Theorized regions of Galápagos macroalgae, based on historical observations and collections. **Barren** = no macroalgal cover; **Crusts** = prostrate, creeping, or crustose growth forms, patches of foliose or branching species; **Foliose/ Diverse** = upright, branching or sheetlike growth forms, high species richness. Macroalgal communities have been reported as diverse and abundant in the Western region, virtually non-existent in the Northern region, and generally dominated by crusts with patchy foliose communities in the central/Southern region. Base map courtesy of D. Ruiz.

Western Region:

Macroalgae of Fernandina Island and the Western coast of Isabela Island are described as "rich, dense, and diverse" (Norris, 1978). Wellington (1975) described this area as having some of the only recognizable macroalgal "communities." In a summary of his field notes, Kendrick (1988a) describes diverse macroalgal communities restricted to lower intertidal and upper subtidal (2-3 m) depths in the Western region, and best developed in exposed locations. He reported species-rich bands of erect, foliose

macrophytes (i.e. *Asparagopsis*, *Spathoglossum*, *Dictyota*, *Dictyopteris*, *Sargassum*, *Corallina, Scinaia*, *Padina*, *Gracilaria*, *Ulva*, *Hypnea*, *Gelidium*, *Laurencia*, *Codium*, and *Kallymenia*) in the shallow subtidal of Fernadina and Western Isabela (Kendrick, 1988a).

One of the earliest and most intensive macroalgal-focused studies was that of William Randolph Taylor (1945), based on a 1934 expedition to the islands. Taylor primarily collected intertidally by hand and subtidally with a dredge, though he noted abundant *Sargassum* (one of the largest and most structurally complex seaweeds in the islands) drifting or washed ashore in the Western region. This observation is corroborated by Garske (2002) who noted large stands of *Sargassum* of one meter in height in shallow waters of Isabela Island. This area also hosts the only known true "kelp" (brown algae in the order Laminariales) in Galápagos: *Eisenia galapagensis* (described by Taylor, 1945), a genus normally found in temperate waters. Solitary individuals were collected by dredging near Isla Santa Cruz (central) by Taylor (1945) but the West coast of Isabela (Western region) was recently found to have extensive "forests" of *E. galapagensis* (Graham, Kinlan, Druehl, Garske, & Banks, 2007). Prior to this discovery, no kelp forests had been described from tropical latitudes, highlighting the globally unique nature of the Western region.

Northern Region:

Macroalgae in the Northern region, specifically around the islands of Darwin and Wolf, has been described as "essentially absent" or "characterized by encrusting corallines and algal turfs" (Wellington, 1975). Not surprisingly, the most conspicuous flora consists mainly of diminutive species of tropical origins, and foliose groups here are represented by *Caulerpa* and *Padina* (Garske, 2002). Larger, branching macroalgae have been reported from deep waters in this region, as dredged from 270 meters by Taylor (1945, see below). In general, the Northern region appears to be macroalgally-depauperate, consisting mainly of pavements of crust-forming species (Dawson, 1964), at least in shallow water.

Central and Southern Region:

Dawson (1964) reported the "general aspect of the seaweed vegetation is one of sparsity. Except for a few species at relatively few localities among Southern islands, the vegetation is not dense or richly developed. Members of the Sargassaceae and Dictyotaceae are the only algae of large size, and these are mainly confined to the South." In this region crusts dominate, and fleshy macroalgae seem to flourish only at very specific localities such as the upwelling-influenced coasts of Floreana and Española islands, where Taylor (1945) found deeper dredging (to 55 m) and intertidal collecting to be particularly productive. He also found dredging in the waters offshore of Puerto Ayora (in Academy Bay, Santa Cruz Island, today the largest settlement in Galápagos) to be "a

spectacular success" while the intertidal collecting yielded very little. Garske (2002) describes this same South/Central region as the most interesting in terms of macroalgae; while individuals are typically smaller and sparser than in the West, communities are composed of a mixture of tropical and temperate species, making this region potentially the most biodiverse.

Quantitative estimates of macroalgal standing stocks to parameterize trophic models have varied more than three-fold between the central/Southern region (256.80 tons.km^{-2} at Floreana Island; Okey et al., 2004) and the Western region (800.48 tons.km^{-2} at Fernandina Island; Ruiz & Wolff, 2011). Contrary to historical records and model parameters, an intertidal herbivory study by Vinueza, Menge, Ruiz, and Palacios (2014) recorded higher initial algal abundances (primarily *Ulva*) at his intertidal site on Santa Cruz (central region), than on Fernandina (Western region). Genovesa (Northern-central) was characterized primarily by crustose coralline algae. These data were collected inside of clustered replicate 30 x 30 cm cages at two nearby sites per island. Due to this design, the discrepancy in algal abundances between those measured and historically observed could be due to small-scale variation (patchiness) in intertidal algal abundances or large-scale regional patterns.

Depth related distribution patterns:

While marine macroalgae are generally most abundant in shallow waters (<20 m), in clear, tropical waters, living macroalgae have been found to depths of 268 m (Littler, Littler, Blair, & Norris, 1985). The deep-water flora of the Canary Islands is known to be particularly abundant and diverse, with new species recently being described and recorded (Haroun, Prud'homme van Reine, Müller, Serrao, & Herrera, 1993; Sansón, Reyes, Afonso-Carrillo, & Muñoz, 2002). Brazilian rhodolith beds and diverse epiphytic communities (including the endemic kelp *Laminaria abyssalis*) span the Equator from 2° North to 25° South, and are common in depths greater than 50m (Amado-Filho, Maneveldt, Manso, Marins-Rosa, & Guimarães, 2007).

The steep-sided volcanic islands of Galápagos offer ample hard substrate into deeper water, and light penetrates far below the thermocline (Dawson, 1964; Graham et al., 2007). Throughout the archipelago, depth related distribution patterns have been described; algae typically flourish at shallower (0-5 m) and deeper (>20 m) depths, while intermediate depths are relatively barren (Kendrick, 1988a). Observations from Southern and Western intertidal and very shallow (1-3 m) subtidal communities describe macroalgae as diverse and abundant, yet depauperate only a few meters below. For example, Kendrick (1988a) describes these shallow depths in the Western region as containing "the richest communities and most luxuriant growths of bladed and branched macroscopic algae."

Taylor's (1945) deeper water dredging (>30 m) was often very productive; a great

deal of his Galápagos collections came from these depths. Of particular interest is his report of collections of *Plocamium* and *Carpomitra* from his Northernmost, and deepest, dredging (183-270 m from Wolf Island). These came from the Northern region where shallower depths (<20 m) are described as relatively barren (see above). Given the less productive and more transparent surface waters in the North, Dawson (1964) speculated that macroalgae there could be more abundant than in the Southern portion of the archipelago at similar depths (Dawson, 1964). Accordingly, during submersible and SCUBA surveys and collections, Norris (1978) often reported abundant deeper water algal communities to depths exceeding 110 ft (33 m). Earle (1980) described a "submergence phenomenon" across the islands: large, foliose macroalgal species found throughout shallow waters in the Western region were only present in the rest of archipelago well below the thermocline (> 20 m depth), where temperatures are colder and more stable.

Also reported from deeper waters is the kelp *E. galapagensis* mentioned previously (Taylor, 1945; Earle, 1980; Graham et al., 2007). Graham et al. (2007) described "forests" of kelp extending beyond the 60 m limits of the expedition's survey methods. This is potentially the most ecologically significant macroalgal community in Galápagos, as *Eisenia* is the physically largest macroalgae so far reported in the archipelago, and presumably one of the most structurally complex biogenic habitats in deeper water.

Role of herbivores:

Marine herbivores are known to greatly impact benthic macroalge (Poore et al., 2012). In the competitive relationship between corals and macroalgae, excluding or removing herbivores from the system causes overgrowth of algae and smothering of corals (e.g. Ogden & Lobel, 1978; Rasher et al., 2012). High abundances of urchins can have an overwhelmingly large influence on the structure of macroalgal communities in both temperate and tropical waters (North & Pearse, 1970; Carpenter, 1985). High-density urchin "fronts" can consume entire kelp forests, leaving behind barren seascapes that may persist for several years (Leighton, 1971; Dayton, 1985; Chapman & Johnson, 1990; Andrew, 1993). In the Canary Islands, the influence of urchin grazing was more important than any other measured environmental variable (temperature, wave exposure, sedimentation, among others) in determining patterns of macroalgal biogeography across the archipelago (Sangil et al., 2011). Herbivorous fish can also influence the structure of macroalgal communities, and are often cited as major controlling factors of macroalgal growth on coral reefs (Choat, 1991; Ojeda & Munoz, 1999).

The role of herbivores (primarily urchins) in driving macroalgal distribution patterns in Galápagos has been proposed by several authors (e.g. Dawson, 1964; Norris, 1978; Wellington, 1984) but remains empirically unconfirmed. Macroalgal grazers in the archipelago consist of reptiles (turtles and iguanas), a diverse group of fish species

(Appendix I), and invertebrates dominated by urchins (Wellington, 1984). Of these, the latter two seem to be in great abundance, possibly enough to have a measureable influence on macroalgal distributions and community composition (Dawson, 1964; Norris, 1978; Kendrick, 1988a).

Common marine herbivores (urchins, fish, iguanas, and crabs) in Galápagos are known to have an influence on algal physical structure and community composition in intertidal and shallow-subtidal habitats; experimental caged plots excluding these consumers experienced rapid blooms of filamentous and bladed macroalgae while control plots remained relatively barren (Vinueza, Branch, Branch, & Bustamante, 2006; Irving & Witman, 2009; Krutwa, 2014). Vinueza et al. (2014) also tested the influence of intertidal grazers (namely urchins, iguanas, and crabs) across productivity gradients in the central and Southern regions of the archipelago. This work found grazing influence on macroalgal community composition and biomass to be most significant at the lowest-productivity site, with less consistent influence at mid-productivity, and little effect at the highest-productivity site. These results could offer insights into the influence of grazers across productivity gradients in subtidal macroalgal assemblages, where herbivorous fish and urchins are much more abundant.

In the Galápagos, the herbivorous fish consist of about 45 species, many of which are obligate herbivores (Appendix I). Damselfish are common in shallow waters, and selectively remove undesirable algal species to create polarized patches of algal filaments (Wellington, 1984). They rigorously defend these algal "gardens" from competing urchins and other fish, and maintain algal habitats in shallow waters (Irving & Witman, 2009). Earle (1980) described the surfaces of rocks at deeper depths (> 20 m) to be covered by a "jungle of red (algae), 15 to 30 cm high," while noting high grazing activity by herbivorous fish (surgeonfish, parrotfish, girellids, blennies, gobies, and others) in warmer, shallow waters (<20 m) above the thermocline. McCosker, Taylor and Warner (1978) noted "a paucity of fishes below the nearshore thermocline." Wellington (1984) described large schools of grazing fish (i.e. *Prionurus* and *Scarus*) and veneers of closely cropped algal mats. These observations and studies underscore the potentially crucial role of herbivorous fish in structuring subtidal algal assemblages across depth ranges. However, little or no quantitative information exists regarding the generality of this phenomenon.

Urchins, particularly *Eucidaris galapagensis*, are currently common and abundant throughout the Galápagos, and are reportedly increasing in numbers (Edgar et al., 2010; Glynn & Wellington, 1983; Ruttenberg, 2001). Glynn and Wellington (1983) speculated that exceedingly high urchin abundances in the Galápagos could be the result of top-predator (shark) removal of urchin predators (pufferfish, wrasses, and triggerfish). Edgar et al. (2010) described geographic ecological trends indicative of a trophic cascade amongst urchins, their predators, and fisheries: decreasing abundances of large predatory fish and lobsters (urchin predators) with proximity to major Galápagos fishing ports, and

a concomitant increase in urchin abundances, is thought to be the result of increased fishing pressure over time in the archipelago.

Indeed, crustose coralline pavements are noted as common in the Galápagos, and in many places have replaced once luxuriant and diverse stands of macroalgae (Kendrick, 1988b; Edgar et al., 2010). These observations are consistent with determinations of fleshy macroalgal cover as being negatively correlated with urchin densities, and urchin abundances declining with both the presence of predators (lobsters and hogfish), and indices of predation (urchin test remains) (Sonnenholzner, Ladah & Lafferty, 2009). Abundances of all of the groups surveyed (macroalgae, urchins, and predators) by Sonnenholzner et al. (2009) were significantly related to fishing, with predators and algae declining, and urchin numbers increasing, along gradients of increasing fishing pressure. Because urchins have an overwhelming influence on macroalgal distributions, even in highly productive upwelling systems (Watanabe & Harrold, 1991; Hernández, Clemente, Sangil & Brito, 2008), urchin abundance should be considered as an important factor in any interpretation of macroalgal biogeography in Galápagos.

TEMPORAL DYNAMICS

Physical and biological influences can dramatically alter macroalgal communities, with cascading effects throughout marine food webs (Mann, 1977; Graham, 2004). These changes can be the result of "regular" seasonal cycles (i.e. ice formation and recession in high latitudes; Barnes, 1999), or anomalous perturbations in coastal ecosystems (i.e. over-fishing, pollution). Seasonally-driven species changeovers of the macroalgal components of benthic communities are common, with measureable influences on associated communities (Foster, 1975; Underwood & Jenakoff, 1984). On coasts in upwelling regions, this shift can happen in a matter of weeks following rapid changes in the parameters of surface waters (Diaz-Pulido & Garzón-Ferreira, 2002; Vinueza et al., 2006).

In Galápagos, wholesale changes in macroalgal community compositions (from fleshy to filamentous) have been anecdotally noted during ENSO events, to the extent of local and widespread extinctions of conspicuous species (Edgar et al., 2010). Given the abundance of herbivores in the system (see "trophic role" section) this change would undoubtedly cause cascading effects through the marine trophic web. The generality of this phenomenon and its potential for long-term residual effects remain unclear, as there is limited quantitative information regarding macroalgal responses to ENSO events in the Galápagos.

There is, however, an abundance of anecdotal evidence of shifts in macroalgal communities as a result of the '82/83 ENSO. Robinson and del Pino (1985) noted a shift in subtidal benthic communities on Floreana to a "monotonous carpet of brown filamentous algae, principally *Giffordia* and *Enteromorpha*." In comparing his 1987

observations in Academy Bay (Santa Cruz Island) to those of Wellington in 1975, Kendrick (1988b) described a long term shift in intertidal community composition. Bladed and branching genera (i.e. *Bifucaria, Grateloupia, Prionitis, Gracilaria, Padina, Spatoglossum*) had been almost entirely replaced by filamentous and crustose forms (i.e. *Cladophora, Chaetomorpha, Giffordia, Ceramium, Polysiphonia, Audouinella*). Through an analysis of the background benthos of itchyofaunal images taken during 1982/'83, Edgar et al. (2010) determined that subtidal cover of filamentous and turf algae did increase significantly, while cover of foliose brown algae declined.

Empirical evidence of the 1997/'98 ENSO-related intertidal macroalgal community changes were recorded by Vinueza et al. (2006). Over the course of an intertidal grazer exclusion experiment in Academy Bay (Santa Cruz Island, central region) control plots, initially dominated by *Gymogongrus*, *Ulva*, and *Enteromorpha*, were replaced during the ENSO event by brown and green filaments (*Giffordia* and *Chaetomorpha*). Shortly after ocean surface temperatures dropped, *Ulva* quickly responded and replaced the filaments, and plots were eventually covered by *Gymnogongrus* (Vinueza et al., 2006). This study highlights the rapid (~ one month) ENSO-induced turnover of the intertidal macroalgal community. While in this case the community ultimately recovered, there is evidence of previous long term changes in intertidal macroalgae following the 1982/'83 ENSO.

Prior to 1982, the large (20-30 cm) fucoid alga *Bifurcaria galapagensis* (Piccone & Grunow) Womersley 1964 was common and abundant in low intertidal and shallow subtidal waters in the Western and Southern regions, sometimes dominating the intertidal and creating mono-specific stands (Wellington, 1975). This relatively large ~ 30 cm alga was recorded in some of the earliest accounts of macroalgae in the archipelago, notably from Isabela Island during the *Hassler* expedition no. 1019, in June of 1872. Over the next century, it was recorded as conspicuous at most of the other islands, from the intertidal to depths of almost 40 m (Taylor, 1945; Silva, 1964; Wellington, 1975). Taylor (1945) reported this alga (then as *Blossevillea*) as the dominant intertidal species on Floreana Island. Silva (1964) reported *B. galapagensis* from five of the largest islands, and it has been recorded in the majority of pre-1982 macroalgal accounts in the archipelago (Taylor, 1945; Dawson, 1964; Silva, 1964; Wellington, 1975). *Bifurcaria galapagensis* was very abundant in the intertidal of Academy Bay up until the 1982 ENSO event. It has not been recorded there since (Kendrick, 1988b). In fact, it has since only been recorded at one site on Floreana Island (Garske, 2002; Edgar et al., 2010), and is listed as Critically Endangered by the global IUCN red list (IUCN, 2016). *B. galapagensis* was not the only macroalgal species to suffer this fate, though due to its large size and intertidal distribution its loss was the most conspicuous. Edgar (2010) also lists six other algal species which, following the '82/83 ENSO, are now most likely extinct.

Thermal stress or nutrient limitation could have driven these changes in

macroalgal abundances, but the influences of herbivores cannot be overlooked. After considering ENSO phases as factors in their analysis of intertidal grazing influence in Galápagos, Vinueza et al. (2014) found grazer effects on algal biomass generally higher during warm phases, particularly at low-productivity sites. Additionally, Carr and Bruno (2013) measured higher grazing rates of Galápagos urchins in mesocosms at elevated temperatures. Urchin grazers therefore could be further compounding the effects of high water temperatures and lower nutrients, creating a situation of intensely negative influence on macroalgal growth during ENSO events. This is particularly relevant given the significant increase (by a factor of two) in *Eucidaris* abundances in the archipelago during and following the '82/83 ENSO event (Edgar et al., 2010).

FUNCTIONAL ROLE

Marine algae are some of the most archaic of the world's primary producers, some being no more complex than plastids and DNA. In shallow temperate waters, macroalgae are a major source of benthic primary productivity and kelp forests, created by brown algae in the order Laminariales, are some of the most productive ecosystems in the world (Mann, 1973). Macroalgae provide direct sustenance to a wide evolutionary range of species. Globally, the macroalgal grazer clade includes marine mammals (sirenians) reptiles (chelonids and squamates), a variety of herbivorous fish (kyphosids, scarids, acanthurids, pomacentrids, siganids, among some others), and a vast array of invertebrates (gastropods, amphipods, decapods, polyplacophorans, echinoderms, among others). Marine subsidies to terrestrial systems in the form of floating macroalgal wrack are a global phenomenon, and offer an important source of organic matter to otherwise nutrient limited (i.e. deserted) island systems (Polis & Hurd, 1996; Krumhansl & Scheibling, 2012). Likewise, sinking macroalgal detritus has been estimated to provide the majority of total particulate organic carbon inputs in deep-water canyons (Harrold, Light, & Lisin, 1998). Decaying macroalgae, the waste produced by herbivores and higher-level consumers in the system, and the decomposing flesh of these consumers is ultimately assimilated by detritivores and microbes. In addition to direct transfer of energy and nutrients, macroalgae offer physical refuges from predation, and can ameliorate light, desiccation, and hydraulic stresses (Dayton, 1975; Fenwick, 1976; Bertness, Leonard, Levine, Schmidt, & Ingraham, 1999; Anderson, 2001; Glasby & Connell, 2001).

Macroalgal grazers are diverse and abundant in the Galápagos. The grazer guild is represented by reptiles, fish, and invertebrates. The most common marine reptiles in the archipelago are the marine iguana (*Amblyrhynchus cristatus*) and the green sea turtle (*Chelonia mydas*), and both feed primarily on macroalgae (Darwin, 1859; Carpenter, 1966; Carrión-Cortez, Zárate, & Seminoff, 2010). Carpenter (1966) describes Punta Espinosa on Fernandina Island, where marine iguanas are particularly abundant, as

having "the largest lizard biomass anywhere in the world." Marine iguanas may be the most visible and iconic of the macroalgal grazers in the Galápagos, but this phenomenal grazer abundance is likely not unique to this species. A search through the Charles Darwin Foundation's (CDF) species checklists cross-referenced with FishBase dietary information identified 45 potential fish grazers (herbivores and omnivores, Appendix I). Some of these species (i.e. *Prionurus laticlavius* and *Scarus ghobban*) have been observed throughout the archipelago in large schools (Wellington, 1984). The aforementioned abundances of grazing urchins in the archipelago also points to the potential importance of macroalgae in the system (Norris, 1978; Wellington, 1984; Kendrick, 1988a).

A trophic model created by Ruiz and Wolff (2011) for the Bolivar Channel in the Western region, depicts macroalgae as a keystone functional group, and estimates a standing stock of macroalgal biomass 25-fold greater than that of phytoplankton in the system. Nine of the 27 higher trophic level (>2.0) functional groups, depend on macroalgal primary productivity, and the total biomass of macroalgal grazers is 43 % of the total consumer biomass. Bottom-up control of this system during ENSO events was modeled by Wolff, Ruiz and Taylor (2012) in the Bolivar Channel (Western region); changes in macroalgal biomasses negatively affected primary consumers, and this effect cascaded through the food web.

A similar model created for Floreana Island in the Southern region resulted in a lower overall importance of macroalge in the system, but a similarly high diversity of grazer functional groups (Okey et al., 2004). This discrepancy could be due to the aforementioned biogeographic differences in macroalgae abundance. While the abundance and diversity of herbivores is one indication of the trophic importance of macroalge in the marine ecosystem of Galápagos, more direct evidence can be found in observed dynamics of these herbivore populations during ENSO events.

ENSO related effects on macroalgal herbivore populations, particularly marine iguanas (*Amblyrhynchus cristatus*), have been highly visible, and well-studied. Because marine iguanas feed almost exclusively on marine macroalgae (Darwin, 1859; Carpenter 1966; Trillmich & Trillmich, 1986), their population characteristics are influenced by the availability of macroagal resources, as was evident over the course of the '82/83 ENSO event (Laurie, 1985). Virtually all iguanas measured over this period by Laurie (1985) ceased growth and lost weight, and some populations experienced 50-70 % mortalities. These effects were thought to be the result of changes in intertidal macroalgal assemblages from diverse, energy-rich, digestible stands of foliose genera like *Ulva*, *Centroceras*, *Gelidium*, and *Spermothamnium*, to mats of low-energy, minimally digestible genera like *Giffordia*. Necropsies of iguanas during this period revealed intestinal impaction by hard, fibrous algal material (likely algal filaments) to be a common cause of death (Laurie, 1985). Macroalgal community shifts during this ENSO, coupled with increased hydraulic energies and higher sea levels (which further restricted

areas available for foraging), undoubtedly contributed to the decline in iguana populations.

DISCUSSION AND FUTURE RESEARCH AVENUES

Distributions:

This review describes a general regional pattern in macroalgal distributions based primarily on anecdotes. We here recommend a concentrated effort to investigate affinities of different macroalgal species or communities to the range of environmental conditions and biotic stressors present in the archipelago. In tropical upwelling regions, macroalgal communities can consist of species with both temperate and tropical affinities, an integration which greatly increases species richness, as evidenced by the ~315 species described in Galápagos (de Guimaraens & Coutinho, 1996; Garske, 2002). This relationship could explain the anecdotal observations of macroalgal biogeographic patterns in the Galápagos Islands; the consistently cold and nutrient rich waters in the West could be the main reason for the apparent relative high abundance of algae in the region. However, depth and herbivore-related influences could be confounding the effects of temperature, and should be included as potential factors in any sampling design.

Nutrient limitation and high temperatures in surface waters are characteristic of ENSO events in the Eastern Pacific (Houvenaghel, 1984; Glynn, 1988; Wolff, Ruiz, & Taylor, 2012), however, the clarity of the water in the Galápagos archipelago allows for light penetration well below the thermocline, to depths generally below the influence of ENSO events (~20 m, Graham et al., 2007). These deeper waters may act as a refuge from potentially growth-limiting changes in temperatures and nutrient levels, and also may harbor undescribed species of macroalgae. Likewise, shallow (0-5 m depth) macroalgal communities have been reported as locally diverse and abundant (i.e. the Western region), and should be sampled thoroughly.

Severe ENSO events have dramatically altered intertidal macroalgal assemblages in the Galápagos, such as the *Bifurcaria* phenomenon described previously (Glynn & Wellington, 1983; Kendrick, 1988b; Vinueza et al., 2006). At such depths, the benthic communities have yet to be extensively surveyed, despite the potential for an abundance of deep-water algal assemblages in the Galápagos (Dawson, 1964).

If present as predicted, these communities could serve important roles in benthic primary productivity and habitat provisioning in the Northern and central regions of the archipelago, where shallow subtidal and intertidal algal assemblages are apparently relatively sparse and species-poor. Here we recommend sampling from the intertidal to a minimum of 30 meters depth (and more if possible) to describe community changes, and quantify depth-related patters across the different geographic regions.

As has been proposed, biotic factors (mainly herbivore influence) could also be influencing distribution patterns. Both urchins and fish grazers are abundant in the

Galápagos, and their influence on macroalgal community structure should investigate on much larger scales (across regions), to elucidate the role of herbivory (or abundances of herbivores) in driving biogeographic patterns.

While other studies have focused on biogeography of more visible and charismatic species in Galápagos, a macroalgal-focused investigation would allow for quantification of potential spatial variation in relationships between macroalgal communities and higher-order trophic structure and function across the archipelago. For example, Edgar et al. (2004) defined specific bioregions based on analysis of fish and macroinvertebrate survey data. Incorporation of macroalgal biogeographic patterns could explain some of these results, particularly for variation in abundances of fish and invertebrate herbivores and their predators. This work could further inform spatially-explicit management schemes, and predict changes in trophic function in the case of macroalgal community declines.

Temporal Dynamics:

Despite potential ecosystem level ramifications, temporal variability in macroalgal communities has yet to be comprehensively studied in the Galápagos. Our understanding of temporal dynamics of macroalgal populations (and associated trophic repercussions) is mostly based on anecdotal observations, with very few empirical studies providing more detailed information. It is known that past ENSO events have caused short-term macroalgal community changeover, long-term elimination of macroalgal species from the archipelago, and devastating effects on iconic, high profile macroalgal grazers like marine iguanas (Edgar et al., 2010).

Nevertheless, our understanding of the effects of both short and long-term climatic variability in Galápagos on most species of macroalgae (and more importantly macroalgal communities and their consumers) remains speculative at best. Data describing current trends in the spatio-temporal distribution of macroalgal species in the archipelago could corroborate observations of past dynamics. Such work would aid immensely in predicting the influence of future ENSO events on macroalgal distributions, community compositions, and overall ecosystem productivity. Creating a large-scale quantitative baseline for macroalgal biogeography and community compositions in combination with long term monitoring of macroalgal dynamics, is of great importance for clearly identifying locations and timing of community shifts. The necessity for seasonal monitoring was emphasized by Kendrick (1986). Coupled with process based experiments to investigate the relationships between environmental parameters and intraspecific physiology and interactions, long-term macroalgal monitoring should be made a priority.

Functional Role:

As previously mentioned, fish and invertebrate grazers are abundant in Galápagos, which highlights the potential importance of macroalgae in the marine ecosystem. The two regionally-based trophic models described above determined macroalgae to be crucial source of productivity, though they produced large differences in biomasses and resultant level of energy contribution relative to phytoplankton productivity (Okey et al., 2004; Ruiz & Wolff, 2011). Due to uncertainties regarding geographic variation in macroalgal biomass and productivity, species-specific differences in energy availability, extra-system transport of macroalgae, and unaccounted for herbivore groups, the validity and generality of this phenomenon remains unclear.

Considering the aforementioned anecdotally described macroalgal distributions throughout the Galápagos, and the allegedly "variable" abundance of macroalgae in the Southern region, the model created by Okey et al. (2004; for the Northern coast of Floreana Island in the Southern region) could have been restricted to an area of relatively low macroalgal biomass compared to the Bolivar Channel in the Western region modeled by Ruiz and Wolff (2011). Additionally, unlike the Bolivar channel model, which measured macroalgal biomass within the system, the standing stock estimates for Floreana were based on measurements from a different island (Santa Cruz, ~60 km to the North), potentially introducing inaccuracy into the biomass parameter. Currently these are the only macroalgal biomass (wet weight standing stock) estimates in existence for Galápagos, but given the uncertainty in their accuracy or generality, it is inappropriate to extrapolate these estimates across the breath of the archipelago. Only a large-scale biogeography and biomass study with effort allocated across the theorized bioregions would provide accurate macroalgal functional group parameters.

Beyond variability in Galápagos macroalgal abundance, more uncertainty in the functional role of macroalgae lies in quantifying its energetic contribution to higher trophic levels. The two models above produced productivity values (Production/Biomass) either arbitrarily (for Floreana) or based on the assumption that Production/Biomass equals total mortality under equilibrium conditions (Bolivar Channel). Regardless, simply quantifying standing biomass of extant macroalgae and using a "mean productivity rate" does not allow for an accurate description of macroalgal trophic function in the system. Macroalgal productivity, caloric values, and palatability (i.e. carbonate or secondary metabolite concentrations) vary by species, and not all species are consumed by all grazer functional groups (Littler & Arnold, 1982; Paul & Hay, 1986; Poore et al., 2012). Therefore community species composition influences the role that macroalgae play in provisioning energy to the system. As such, investigations of macroalgal productivity in Galápagos should be performed across geographic regions, encompass oceanographic phases (e.g. seasonal through ENSO cycles), and account for species-specific energetic contributions.

Another factor confounding our understanding of the function of macroalge in Galápagos is the potential abundance, diversity, and grazing effect of macroalgal mesograzers. Mesograzers (< 25 mm) can be abundant and diverse in macroalgal habitats, and have been shown to structure macroalgal communities via selective grazing (Berthelsen, 2014). Previously only macroinvertebrates (> 20 mm) were considered when creating trophic webs for Galápagos, ignoring both the biomass and secondary productivity of the potentially important mesograzer functional group.

Macroalgae in Galápagos, large phaeophytes in particular, could be responsible for substantial cross-system subsidies, with floating (i.e. *Sargassum*) and sinking forms (i.e. *Esenia*) able to be transported completely out of the system, offering organic enrichment far from their growth area (Krumhansl & Scheibling, 2012). The complex ocean currents flowing throughout the archipelago readily offer a vector for transport for floating wrack, and sinking detritus can quickly reach a thousand meters on the steep Western and Southern seafloor slopes. In addition to passive transport, the Galápagos experiences a very unique form of cross-system macroalgal transport via the marine iguana. After grazing in the intertidal and shallow subtidal, these reptiles typically defecate while basking on shore, transporting this energy source out of the subtidal realm and creating a potentially important source of organic matter to the otherwise barren volcanic islands (Carpenter, 1966). The potential significance of such cross-system transport of algal productivity, particularly for the younger, more barren islands in Galápagos, warrants further investigation.

The largest phaeophyte genera in Galápagos, specifically *Sargassum* and *Eisenia*, can attain lengths of over one meter (Garske, 2002; Graham et al., 2007). *Sargassum* is densely branched and structurally complex, and elsewhere serves as vital habitat to hundreds of species (Coston-Clements, Settle, Hoss, & Cross, 1991). These include larvae, recruits, and juveniles, which use the algae as a nursery habitat. Large macroalgal species are likely functioning similarly in Galápagos, and if so, changes in macroalgal community structure like those noted during ENSO events could have indirect ecological effects reaching beyond the food web. Studying the significance of macroalgal habitats in Galápagos, could yield further functional role insights.

Conclusions and outlook:

Given the current paucity of investigations focusing on the macroalgae of Galápagos, there is a plethora of additional research avenues in ecology, evolution, and systematics. Higher-order ecological relationships have received some empirical attention, such as important influences of grazers on macroalgal identity (Irving & Witman, 2009; Brandt, Witman, & Chiriboga, 2012; Vinueza et al., 2014). These investigations yielded ecologically interesting results, but with the exception of the work of Vinueza (2014), the generality of findings across productivity gradients, and stability over time, has yet to be determined. Given the abundance of grazers and higher-order

predators in the system, the importance of these ecological relationships in a trophic web framework should be considered.

Evolutionarily, Galápagos macroalgae offer a range of opportunities for research, including trans-archipelago and continental phylogenetic relationships (estimates of endemism among the taxa range upwards of 40 %, but comprehensive continental taxonomic studies are lacking, particularly in Ecuador and Colombia). The influence of macroalgae on the evolution of certain endemic fauna, particularly the marine iguana, has also yet to be investigated. Molecular evidence suggests that the continental ancestors of the marine iguana may have arrived on presently submerged volcanoes as much as 10 million years ago (Rassmann, Tautz, Trillmich, & Gliddon, 1997). One can imagine that the newly emerged volcanic islands were essentially barren above the surface, with a potentially lush cover of macroalgae in shallow water (much like Fernandina Island today) offering an abundant source of energy and ultimately selectively forcing the evolution of these unique marine reptiles.

Overall, the Galápagos is rife with opportunities for macroalgal investigations. However, given the historically theorized relationship between declining macroalgal productivity and grazer population crashes during ENSO events, priority should be placed on determining baselines of community compositions, biomasses, and productivities throughout the archipelago. Long-term monitoring of these parameters in parallel with the abundance, identity, and health of associated grazers would provide clear evidence of the true trophic role of macroalgae in Galápagos. This could serve as a rapid assessment of the health of the nearshore marine ecosystem, and inform model-based predictions of future ecological change.

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Chapter 2: Variation in macroalgal community functional group composition and diversity across the Galapagos archipelago

Abstract

Describing patterns in the compositions and spatial distributions of plant communities provides the foundation for mechanistic investigations, and provides understanding of the role these communities play in structuring energy flows through ecosystems. In coastal marine ecosystems, macroalgae (seaweeds) are an important source of primary productivity, and provide habitat for a range of marine animals. Macroalgal distributions are limited in space and time, and distribution patterns are readily apparent across oceanographic boundaries. Tropical upwelling systems are particularly interesting in terms of marine biogeography, though many remain unstudied. Macroalgae have been reported as locally diverse and abundant in the Galapagos archipelago, and regionalization has been anecdotally described. Here, a methodical, large-scale survey effort was undertaken to quantify variation in functional composition (9 group scheme) of macroalgal communties across the archipelago. Overall, communities are dominated by the "Calcareous Crustose" functional group, and dissimilarity across transects was driven by differences in cover of this group. Surveys were conducted at two depths (6 and 15m), and though there was no difference in functional group diversity across depths, results showed significantly higher cover of the 'Thin Foliose' group in shallower water. A three-region scheme is suggested based on overall characteristics: the 'West' is more diverse and unique, and along with the 'North,' had lower overall cover of 'Crustose Calcareous'. The 'Cental/South' had overall high cover of 'Crustose Calcarous,' and locally high cover of 'Filamentous, and 'Microalgae.' These results can be used as a baseline for future changes in macroalgal community structure, and to to more accurately quantify regional-scale differences in macroalgal community biomasses and productivities.

Keywords: Macroalgae, functional ecology, Galapagos, functional groups, community composition

INTRODUCTION

Studies of the spatial distributions of species are a foundation of ecology. Describing distributional patterns of species and communities provides the basis for mechanistic ecological investigations into potential influential factors. All life on earth depends in some way on primary productivity, and due to interactions between species and the environment, plant community compositions vary in space and time (Watt, 1947). This variation can be the result of bottom-up, top-down, and sideways influences acting independently or interacting (Turner, 1989, Ripple et al., 2001). Because variation in plant communities directly influences the resources available to higher trophic levels, understanding the structure and function of plant communities has long been a goal of ecology (Silvertown & Law, 1987; McGill et al., 2006).

Patterns of terrestrial plant community compositions have been described at both large and small scales (e.g. Von Hubmolt, 1807; Herben et al., 1993). High-latitudes are typically tundra-dominated, and plant communities generally transition from coniferous to deciduous to tropical forests with decreasing latitude. Variation in altitude, topography, precipitation, soil composition, disturbance, and herbivory can can greatly influence this general pattern (Watt, 1947).

Our understanding of the limitations of plant distributions is not limited to terrestrial systems. Plant distributional patterns in the oceans are also driven by some of these factors, while others are unique to the marine realm. For example, terrestrial and marine primary productivity are both generally limited by nitrate and phosphorous availability (Elser et al., 2007). However, while terrestrial plants can thrive at a wide range of altitudes, marine production is generally limited to the first 60 meters of the water column due to light dissipation (Yarish & Kirkman, 1990; Markager & Sand-Jensen, 1992). In shallow coastal marine ecosystems, macroalgae (seaweeds) are an important source of primary productivity, and provide habitat for a range of marine animals (Mann, 1973; Dayton, 1985). However, environmental and biological factors limit macroalgal distributions in space and time and extrinsically alter the ecosystem services these algae provide to associated biological communities (Bustamante & Branch, 1996, Bischof et al., 2006).

The most obvious ecosystem service provided by different species of macroalgae is primary production, a variable limited by the intrinsic characteristics of different species (Litter, 1980). These characteristics include external and internal structure, and cellular chemistry (Steneck & Deither, 1994). Mostly due to the relationship between production and morphology, functional groupings of marine algae have classically been based on gross form, a practice criticized for assuming generalization of these properties across all species within a group (Padilla & Allen, 2000). However, since macroalgal production is generally related to overall size and complexity of macroalgal species,

variation in the gross morphologies of species within macroalgal communities will influence the overall primary production of the benthos.

Generally, macroalgal communities are most diverse, productive, and structurally complex on shallow rocky reefs in cold-temperate waters, where they can dominate hard benthos (Kerswell, 2006). The physically largest and most structurally complex macroalgal species (kelps) are generally restricted to these regions (Dayton, 1985). By comparison, tropical macroalgal communities are generally thought to be relatively simplistic, and often spatially limited by competition with corals (Jones et al., 1987). Composed of physically smaller and less complex species, and contributing only minimally to overall system productivity and habitat provisioning, the ecology of tropical macroalgal communities has historically been of relatively little interest.

Diverse, robust, and complex macroagal communities have been found in low-latitude upwelling systems, where they exist in stark contrast to adjacent "barren" seafloor regions, or coral-dominated shallow benthos. Examples where this pattern has been described include the Canary Islands in the Atlantic Ocean (Sangil et al., 2011), the Scocotro Archipelago in the Indian Ocean (Schils & Coppejans, 2003), and the Galapagos Islands (Tompkins & Wolff, 2017), where over 300 species of macroalage have been described.

The Galapagos Islands are an upwelling-influenced archipelago spanning the equator in the Pacific Ocean, and are located at the confluence of several oceanic currents. Galapagos experiences geographic and seasonal fluctuations in surface water temperatures (Palacios, 2004), and previous studies have described marine biogeographic regions with unique communities of seabirds, fish, and macroinvertebrates (Harris, 1969; Edgar et al., 2004). Galapagos macroalgal communities may be ecologically important, but remain relatively unstudied at large scales (Tompkins & Wolff, 2017).

A Galapagos macroagal regionalization scheme consisting of three bioregions (West, North, and Central/South) was posited by Tompkins & Wolff (2017). This scheme was based primarily on anecdotal information, with both environmental and biological factors presented as possible influences. This review described both geographic and depth-related patterns in macroalgal abundances and community compositions, and provides the foundation for the present study. Here we seek to quantitatively describe any extant geographic regionalization of macroalgal functional communities in the Galapagos Islands; archipelago-wide dissimilarities in benthic cover of macroalgal functional groups on shallow subtidal reefs across two depth strata will be described and compared to previously described marine bioregions.

Specifically this work will:

1) Establish a functional-group approach to describing macroalgal community composition in the Galapagos.

2) Determine the functional groups most responsible for dissimilarity in macroalgal community structure between sites across the archipelago, and determine a best-fit model for grouping sites based on dissimilarity.
3) Identify and quantify depth-related differences in macroalgal functional group composition and diversity, and test if depth-related differences within sites would change the grouping scheme determined previously.
4) Test the relationship between functional group diversity and cover of dominant groups.

METHODS

Study Area and Site Selection

The Galapagos Islands are an upwelling-influenced tropical archipelago spanning the equator, located approximately 1000 km West of the Ecuadorian coast in South America (Figure 1).

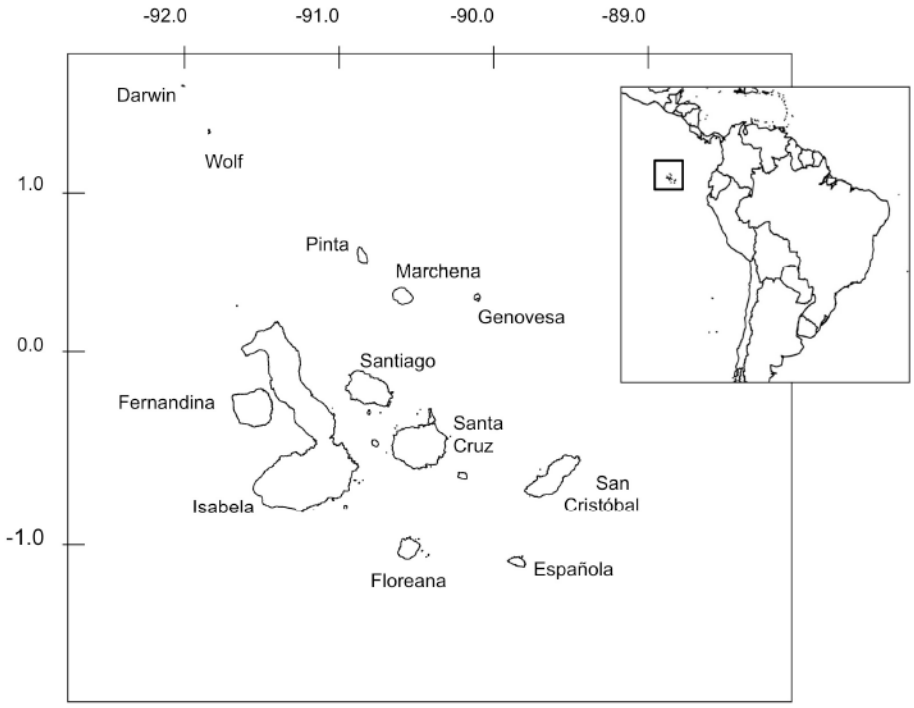

Figure 1: Location of Galapagos Archipelago, and main island names.

Site surveys were conducted during and in collaboration with the ecological monitoring program of the Charles Darwin Foundation (CDF), and during sediment sampling of the COGA (Carbonate Organisms of the Galapagos Archipelago) project. Whenever possible, effort was distributed throughout previously described marine bioregions of the

archipelago (Far north, West, South-Central, and Bahia Elizabeth; Edgar, Tompkins & Wolff). The coastline within and around Academy Bay (Santa Cruz Island) offered logistically easier access, and was therefore more thoroughly surveyed.

Surveys

Benthic surveys were conducted as per the methodology of the CDF marine ecological monitoring program for sessile organisms, as this data was to be shared. At each sampling site, at each of 6 and 15 meter depths (the maximum diving depth permitted by safety regulations), a 50-meter transect was laid parallel to the coastline. In some cases, only one transect per site was logistically feasible, mostly due to high current or surge, or simply a lack of substrate (tops of deeper pinnacles or seamounts). Every five meters along each transect, an 80-intersect gridded quadrat was placed on the seafloor and the primary substrate holder beneath each intersection point was recorded for a total of 800 points per transect.

Functional Groups

Here we developed a functional grouping scheme based on those posited by Littler and Littler (1980), and Steneck and Dethier (1994), which reflects the macroalgal functional groups present in the Galapagos:

Functional Group Definitions (full list of species and groupings in Appendix II).

'Microalgae': Algae forming visible mats or turfs, but not obviously filamentous. Includes cyanobacteria and chain-forming diatoms.
'Filamentous': Clearly visible, uni-or multiseriate filaments not forming blades.
'Thin Foliose': Mono-or distromatic, broad (> 2cm) fronds (blades).
'Thick Foliose': Corticated and broadly bladed or widely branched.
'Corticated Branching/Bushy': Thick, densely branched.
'Leathery'': Thick, densely corticated, bladed or widely branched; typically phaeophytes (Ochrophyta).
'Articulated Calcareous': Geniculate (or articulated) calcareous.
'Calcareous Crustose': Non-branching (non geniculate), prostrate, calcium carbonate-based algae. Includes basal portions of geniculate forms.
'Non Calcareous Crustose': Prostrate, unbladed and unbranched, or basal or initial forms of non-calcium carbonate based groups (i.e. *Hildenbrandia* or creeping, unbladed growth forms of *Lobophora*).

Data Analysis

As this study focused on macroalgal communities, any non-algal (sand, bare rock, sessile invertebrate, etc) data points were subtracted from the data before analysis. Percent cover of functional groups per site and per transect was determined by dividing the points per functional group by the total points in that site or transect, and multiplying by 100.

All statistical analyses, unless otherwise stated, were performed in R. For both pooled (per site) and individual transect data (per depth), normality of the raw and transformed data was assessed using the R package MVN (MultiVariate Normality). In both cases, and using cover data as variables and sites or transects as factors, non-parametric principal component analyses (PCA) were used to determine which variables were most important for community structure, non-metric multidimensional scaling (NMDS) was used to compute and plot overall differences between sites and visualize potential groupings, and cluster analyses were performed to determine the best-fit model for groupings (identity and number). All multivariate analyses were performed using the VEGAN package in R. Tukey's HSD t-tests were used to test for differences in individual functional group cover and overall functional group diversity between depths. Simple linear regression was used to investigate the relationships between individual functional group cover and functional group diversity. All variance (±) is presented as Standard Deviation (SD) unless otherwise indicated.

RESULTS

Surveys were conducted between June of 2012 and April of 2014. In total, data was collected from 50 transects at 30 sites throughout the archipelago (22 transects at 6m, and 28 transects at 15m; Table 1, Figure 2). While attempts were made to collect as much data as possible, due to a combination of logistic limitations, environmental factors, and safety precautions, data was not collected from both depths at all sites.

Table1: Survey site information.

Survey Date	Island	Location	Depth (m)	Transect Code	Latitude (dd.dd)	Longitude (dd.dd)
24-Jun-12	Pinta	Cabo Ibetson	15	PI00(15)	0.544067	-90.720545
24-Jun-12	Pinta	Cabo Ibetson	6	PI00(6)	0.543724	-90.720062
24-Jun-12	Pinta	Turismo	15	PI01(15)	0.542564	-90.73154
24-Jun-12	Pinta	Turismo	6	PI01(6)	0.543123	-90.73126
25-Jun-12	Wolf	Corales	15	WO01(15)	1.387035	-91.816351
25-Jun-12	Wolf	Corales	6	WO01(6)	1.38684	-91.816495
25-Jun-12	Wolf	Fondeadero	15	WO05(15)	1.382773	-91.819156
25-Jun-12	Wolf	Fondeadero	6	WO05(6)	1.382999	-91.81907
26-Jun-12	Darwin	Arricife[1]	15	DA00(15)	1.674647	-91.992228
26-Jun-12	Darwin	Fondeadero	15	DA01(15)	1.680847	-91.999286
26-Jun-12	Darwin	Fondeadero	6	DA01(6)	1.680662	-91.999585
28-Jun-12	Isabela	Cabo Marshall	15	IS01(15)	-0.01605	-91.208285
28-Jun-12	Isabela	Cabo Marshall	6	IS01(6)	-0.01792	-91.20808
31-Jul-12	Santa Cruz	Los Dedos[1]	15	SC13(15)	-0.747924	-90.285848
31-Jul-12	Santa Cruz	Punta Estrada	15	SC14(15)	-0.759883	-90.303288
9-Aug-12	Santa Cruz	Punta Estrada	6	SC14(6)	-0.760465	-90.304145
9-Aug-12	Santa Cruz	Punta Nunez[1]	15	SC15(15)	-0.749131	-90.244348
27-Aug-12	Santa Cruz	Islote Caamano	15	SC12(15)	-0.75807	-90.279552
27-Aug-12	Santa Cruz	Islote Caamano	6	SC12(6)	-0.758182	-90.279311
12-Sep-12	Santa Cruz	El Bajo[2]	15	SC11(15)	-0.762702	-90.292153
16-Mar-13	Santa Cruz	Canal Itabaca 1[2]	6	SC08(6)	-0.479012	-90.260005
16-Mar-13	Santa Cruz	Canal Itabaca 2[2]	6	SC09(6)	-0.48758	-90.300139
19-Mar-13	San Cristobal	Manzanillo	15	SB10(15)	-0.84717	-89.552083
19-Mar-13	San Cristobal	Manzanillo	6	SB10(6)	-0.847662	-89.551141
20-Mar-13	San Cristobal	Isla Lobos8[1]	15	SB06(15)	-0.854566	-89.565577
20-Mar-13	San Cristobal	Las Tijeras	15	SB09(15)	-0.886973	-89.607646
20-Mar-13	San Cristobal	Las Tijeras	6	SB09(6)	-0.887626	-89.607646
21-Mar-13	Espanola	Cerro Colorado	15	ES02(15)	-1.378044	-89.633752
21-Mar-13	Espanola	Cerro Colorado	6	ES02(6)	-1.37844	-89.6236
21-Mar-13	Espanola	Bajo Gardner[1]	15	ES03(15)	-1.34813	-89.6366
21-Mar-13	Espanola	Isla Gardner	15	ES12(15)	-1.340881	-89.648845
21-Mar-13	Espanola	Isla Gardner	6	ES12(6)	-1.341775	-89.6484
22-Mar-13	Floreana	La Botellita[2]	15	FL04(15)	-1.28889	-90.49712
22-Mar-13	Floreana	Las Cuevas	15	FL06(15)	-1.232859	-90.419785
22-Mar-13	Floreana	Las Cuevas	6	FL06(6)	-1.23299	-90.42027
22-Mar-13	Floreana	Punta Cormoran	15	FL13(15)	-1.225459	-90.419329
22-Mar-13	Floreana	Punta Cormoran	6	FL13(6)	-1.225459	-90.419916
23-Mar-13	Isabela	Caleta Derek	15	IS24(15)	-0.685145	-91.260954
23-Mar-13	Isabela	Caleta Derek	6	IS24(6)	-0.687407	-91.259789
24-Mar-13	Isabela	Bahia Urvina[1]	15	IS42(15)	-0.397698	-91.240256
29-Mar-13	Isabela	Caleta Iguana	15	IS41(15)	-0.960607	-91.453447
29-Mar-13	Isabela	Caleta Iguana	6	IS41(6)	-0.959042	-91.449554
1-Apr-13	Fernandina	Cabo Douglas	15	FE01(15)	-0.302022	-91.653338
1-Apr-13	Fernandina	Cabo Douglas	6	FE01(6)	-0.301562	-91.653385
1-Apr-13	Fernandina	Punta Espinosa	15	FE03(15)	-0.261707	-91.445664
1-Apr-13	Fernandina	Punta Espinosa	6	FE03(6)	-0.262194	-91.445241
3-Apr-13	Santa Cruz	El Eden	15	SC07(15)	-0.559754	-90.540986
3-Apr-13	Santa Cruz	El Eden	6	SC07(6)	-0.559762	-90.54014
3-Apr-13	Santa Cruz	Cerro Dragon	15	SC10(15)	-0.521995	-90.491002
3-Apr-13	Santa Cruz	Cerro Dragon	6	SC10(6)	-0.523664	-90.489765

[1]Only one transect surveyed because of strong surge or current.

[2]Bathymetry of site only permitted transects to be surveyed at one depth.

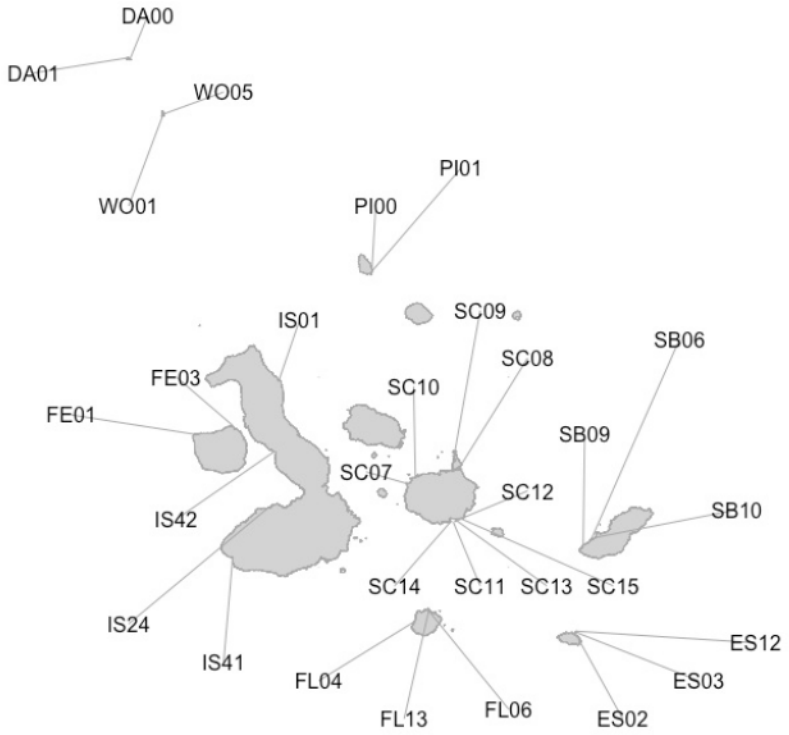

Figure 2: Location and codes of survey sites. Site labels correspond to transect codes used in all tables and figures. Depth was omitted for clarity.

Functional Groups

'Microalgae': Two distinct main groups were noted. These were small (3-6cm diameter) tufts of filamentous (2-4 cm length) cyanobacteria, e.g. *Lyngbya* (Cyanophyceae), or mats of benthic, chain-forming diatoms. This group was relatively rare in Western sites, and most common in the Central region (highest at Cerro Dragon on Santa Cruz Island). This was perhaps the most ephemeral group, as many of the diatom mats seemed loosely connected to the substrate. This group was more indicative of "degraded" sites, which were characterized by high cover of diatom mats.

'Filamentous': Very common, and recorded as red (*Ceramium*, *Polysiphonia*) green, and occasionally brown (*Giffordia*, *Ectocarpus*) filaments. This group was regularly recorded in active damselfish (*Pomacentridae*) nests, which tended to consist of polarized (monospecific) filaments, and were usually located in shallower water (6m transect).

'Thin Foliose': Common, particularly in shallow transects. Recorded mainly as dense, cropped (grazed to 1-2 cm maximum height) cover of *Ulva* in Western and central/Southern sites. In the North, recorded mainly as patches of a small (5-8 mm), delicate species of *Dictyota* (possibly *D. grossedentata*).

'Thick Foliose': Recorded mainly as *Kallymenia, Padina, Rhodymenia,* larger *Dictyota spp.*, and foliose forms of *Lobophora*. More often found in deeper water (15m), particularly in the Western sites.

'Corticated Branching/Bushy': Recorded primarily as a variety of reds: *Hypnea, Gymnogongrus, Prionitis, Laurencia, Gelidium*. Also recorded as *Sargassum* in Western sites.

'Leathery'': Least common group. Primarily recorded as *Spathoglossum.* Only recorded in Western sites, though noted in shallower waters < 5m at several sites in the Central/Southern region.

'Articulated Calcareous': Uncommon. Recorded as small patches of *Jania* and *Amphiroa*, of 1-2.5 cm maximum axial extension.

'Calcareous Crustose': Ubiquitous, most common group. Recorded exclusively as species of crustose (non-geniculate) coralline algae (Corallinales).

'Non Calcareous Crustose': Commonly recorded in the Northern sites, though present to some degree in most transects. Mostly recorded as *Hildenbrandia*, *Pessonelia*, *Ralfsia*, or dense, creeping, unbladed growth forms of *Lobophora*. Occasionally encountered as very dense, prostrate or basal forms of *Codium*.

Normality and Variance of Data

A Mardia's Multivariate Normality Test failed due to extremely skewed data (g1p = 187.5779, chi.skew = 1563.15, p = $4.696645e^{-226}$; Appendix II).

Square root, 4^{th} root, and Chi-squared transformations also failed normality tests due to skewness. This was likely due to the overwhelming dominance of the 'Calcareous Crustose' group (Figure 5), and the relative scarcity and patchiness of other groups (e.g. 'Leathery' and 'Articulate Calcareous'). Therefore, non-parametric statistical analyses were used for the multivariate tests.

Data by site (transects pooled per site)

In general sites were dominated by the 'Calcareous Crustose' functional group (Figure 3). Cover ranged from 9.76% at Cabo Douglas (Fernandina, FE01) to 86.98% at Manzanillo (San Cristobal, SB10), with an overall (all sites pooled) mean of 57.94% ± 20.49 (Figure 4). At 21 of the 30 sites, the 'Calcareous Crustose' functional group was recorded at >50% cover.

Other functional groups dominated at various sites. 'Thin Foliose' was recorded covering 59.74% at Caleta Derek (Isabela, IS24), and greater than 50% cover of 'Filamentous' was recorded at both sites in Canal Itabaca (SC08, SC09), between Santa Cruz and Baltra Islands. In other cases a more even distribution of cover across multiple groups was recorded, and lack of clear dominance of any particular group was recorded at Cabo Douglas (Fernandina, FE01), Fondeadero (Darwin, DA01), and Corales (Wolf, WO01).

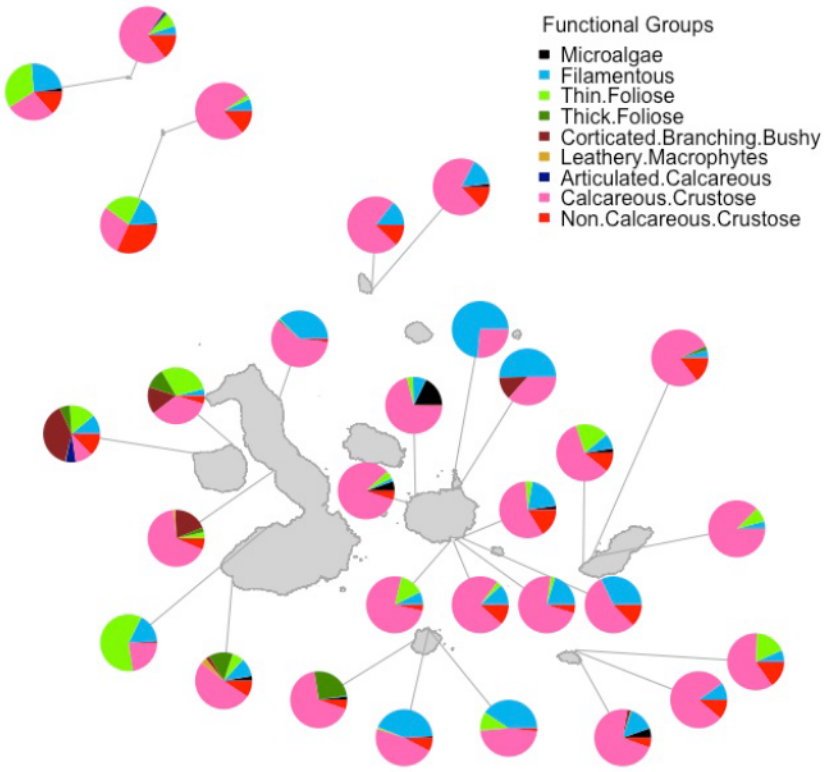

Figure 3: Percent cover of macroalgal functional groups at each survey site (n=50).

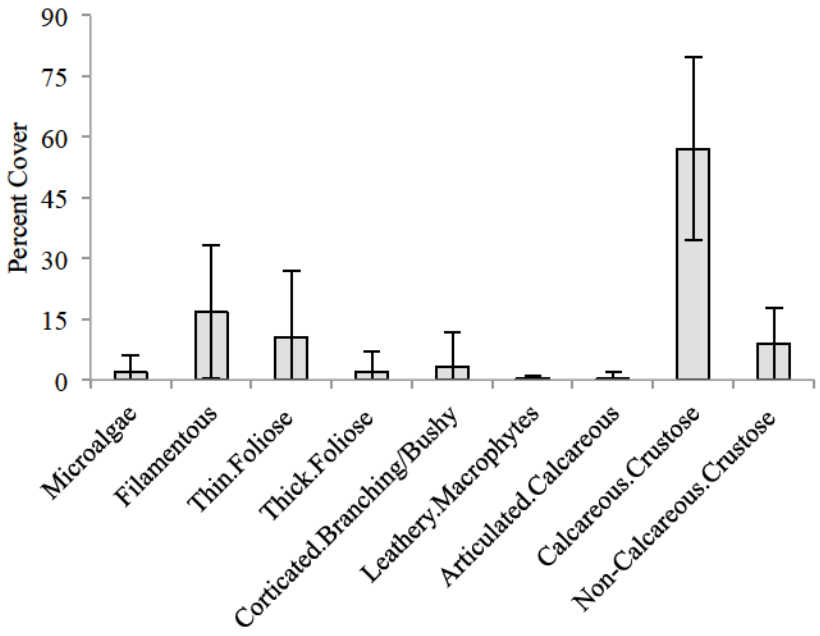

Figure 4: Overall mean (all sites pooled) percent cover of functional groups. Error bars represent standard deviations.

Presence and Diversity per Site

At no site were all functional groups recorded. Functional group diversity per site varied from 2 to 8 groups, and averaged 4.77 groups (± 1.36). 8 groups were recorded at Caleta Iguana (IS41) and Cabo Douglas (FE01), while only 2 groups were recorded at Canal Itabaca (SC09).

'Crustose Calcareous' was the most commonly recorded group, and was present at all 30 sites surveyed. Recorded in order of descending presence were 'Filamentous' (29 sites), Non-Calcareous Crustose (28 sites), 'Thin Foliose' (22 sites), 'Microalgae' (13 sites), 'Thick Foliose' and 'Corticated Branching/Bushy' (7 sites each), 'Articulated Coralline' (4 sites), and 'Leathery' (3 sites).

Principal Components Analysis

For by-site percent cover data, principal component loadings were as such: 'Calcareous Crustose' loaded positively on PC1, and accounted for 55.1% of total variance; 'Thin Foliose' (+) and 'Filamentous' (-) groups loaded primarily on PC2, and accounted 26.70% of total variance; PC3 and PC4 accounted for 9.26 and 4.99% of the total variance, respectively (Figure 5).

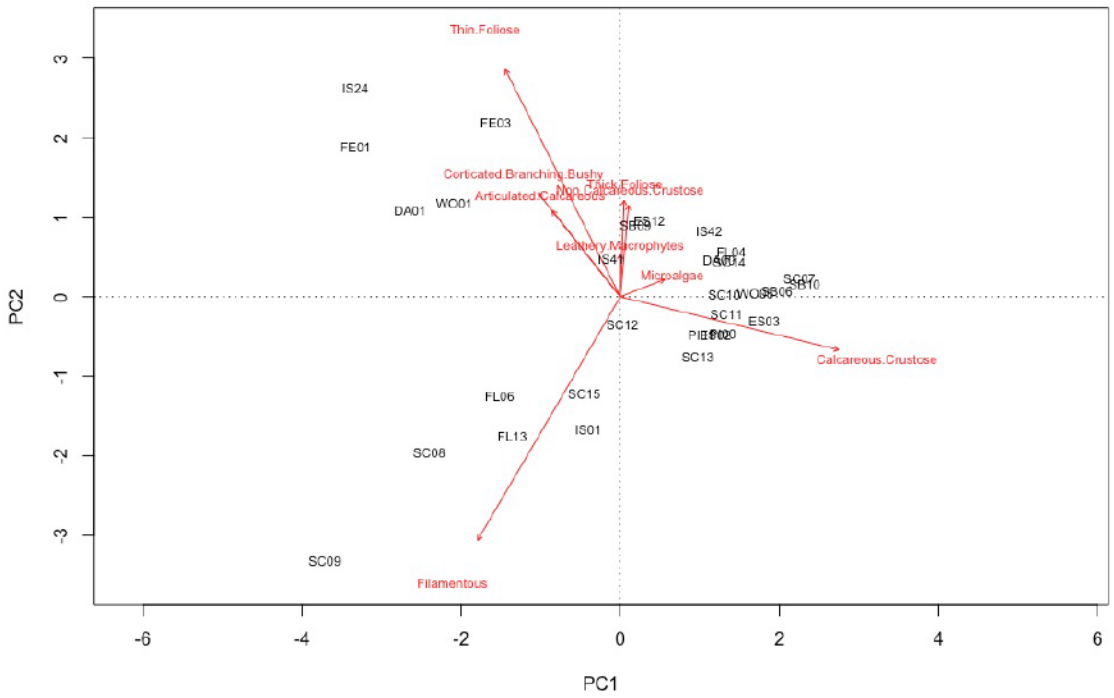

Figure 5: Non-metric PCA plot of sites (pooled data). Black labels are Transect Codes (Table 1, Figure 2), red labels are macroalgal functional groups (Factors).

Cluster Analysis

Two groups explained 48.84% of variability in the cluster analysis, which provided the best-fit model (Figure 6). Further groupings in order of descending percentage (%): 4 groups (48.50), 3 groups (46.37), 5 groups (47.36), 6 groups (43.99), 7 groups (44.80), 8 groups (44.62), 9 groups (42.13), and 10 groups (42.04).

In the best-fit model (2 groups) one group consisted of five sites, and in order of within-group decreasing dissimilarity (increasing similarity) included: Cabo Douglas (Fernandina, FE01), Punta Espinosa (Fernandina, FE03), Caleta Derek (Isabela, IS24), and (equally dissimilar) Fondeadero (Darwin, DA01) and Corales (Wolf, WO01). All other sites grouped separately. Interestingly, within that second group (25 total sites), there was a clear sub-group consisting of (in order of decreasing dissimilarity): SC08 and SC09, IS01 and SC15, FL06 and FL13. These sites were more dissimilar based on their high 'Filamentous' cover.

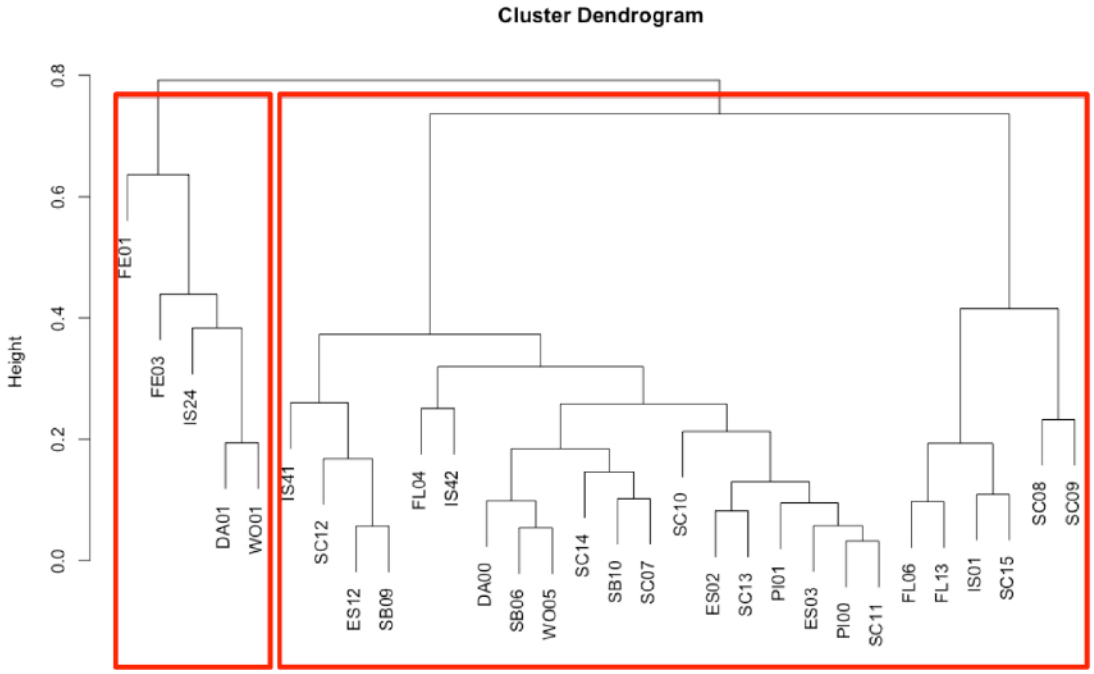

Figure 6: Cluster dendrogram of all sites, with best-fit groupings outlined in red (pooled data). Labels are Transect Codes (Table 1, Figure 2).

Data by Transect (6 and 15 meter depths)

Data was collected from 22 transects at 6m depth, and from 28 transects at 15m depth (Table 1). In general, transects were dominated by the 'Calcareous Crustose' functional group (cover ranged from 4.87-96.67%, overall mean of 57.01%; Figure 7). >50% cover of 'Calcareous Crustose' was recorded at 33 transects (66% of all transects). >50% cover of 'Calcareous Crustose' was recorded at 11 (50%) of transects in 6m depths, and at 22 (78.6%) of transects in 15m depths.

Across all transects, the cover of most groups did not vary with depth (Figure 10, Table 2). However, overall mean cover of 'Thin Foliose' algae was greater on the shallow transects (17.53% in 6m vs. 4.80% in 15m, $p = 0.014$; Figure 7).

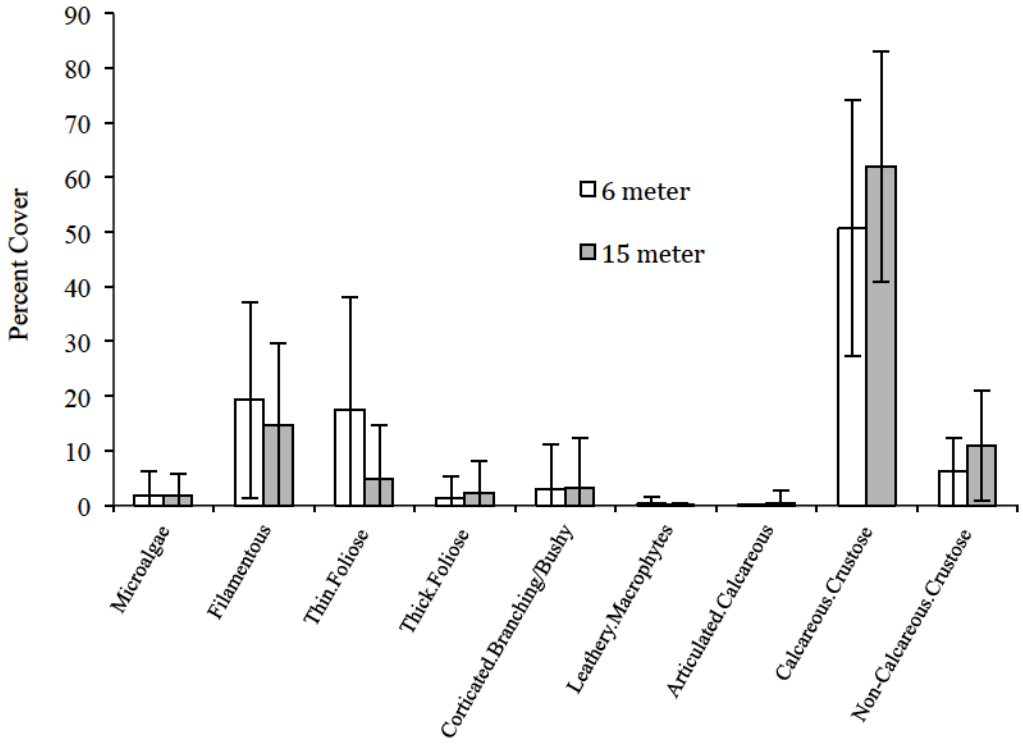

Figure 7: Mean percent cover of functional groups by depth. Error bars represent standard deviations. White bars: 6 meter depth; grey bars: 15 meter depth.

Table 2: Mean % cover at 6 and 15 meter depths and adjusted p-values for Tukey HSD t-tests per functional group.

Functional Group	6m % cover	15m % cover	p adj
Microalgae	1.84	1.73	1
Filamentous	19.29	14.59	0.984183
Thin Foliose	17.53	4.80	0.0142591
Thick Foliose	1.24	2.36	1
Corticated Branching/Bushy	2.96	3.08	1
Leathery	0.29	0.08	1
Articulated Calcareous	0.05	0.48	1
Calcareous Crustose	50.71	61.97	0.0634073
Non-Calcareous Crustose	6.12	10.91	0.9926488

This trend (higher cover in 6m of 'Thin Foliose') can be clearly seen at several sites (Figure 8), e.g. Punta Espinosa (Fernandina, FE03), Caleta Iguana (Isabela, IS41), Las Tijeras (San Cristobal, SB09), Corales (Wolf, WO01), Punta Estrada (Santa Cruz, SC14), and Isla Gardner (Espanola, ES12).

While not statistically significant ($\alpha = 0.05$) cover of 'Calcareous Crustose' algae was generally greater on the deeper transects (61.97% at 15m vs. 50.71% in 6m, $p = 0.063$;

Figure 10, Table 2). Examples of this trend include Punta Espinosa (Fernandina, FE03), Cabo Marshal (Isabela, IS01), Caleta Iguana (Isabela, IS41), Manzanillo (San Cristobal, SB10), and Las Tijeras (San Cristobal, SB09).

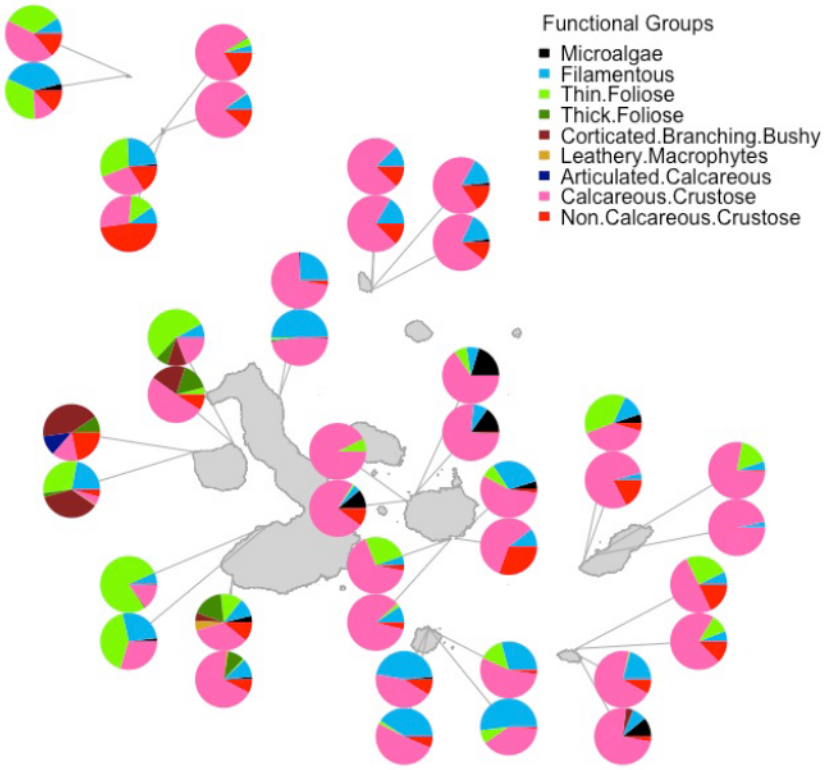

Figure 8: Percent cover of macroalgal functional groups per transect, at sites where data was collected at both 6 and 15m depths. For clarity, sites where data was collected from only one transect were omitted (but are included in Figure 6). Charts are stacked vertically per site: the upper chart represents the 6m (shallow) transect, and the lower chart represents the 15m (deep) transect.

Presence and Diversity per Transect

Across all transects, functional group diversity varied from 2 to 8 groups, and averaged 4.34 groups (±1.26). At the extremes of this range, 8 groups were recorded at Caleta Iguana (Isabela, IS41) and Cabo Douglas (Fernandina, FE01), while only 2 groups were recorded at Canal Itabaca (Santa Cruz, SC09).

'Crustose Calcareous' was the most commonly recorded group, and was present at all transects surveyed (100% of transects, Figure 9). Recorded in order of descending presence were 'Filamentous' (46 total transects), Non-Calcareous Crustose (43 transects), 'Thin Foliose' (32 transects), 'Microalgae (17 transects), 'Thick Foliose' and 'Corticated Branching/Bushy' (10 transects each), 'Articulated Coralline' (5 transects), and 'Leathery' (4 transects). Differences in functional group presence across depths was greatest for the 'Calcareous Crustose' group, which was more commonly recorded in deeper depths (92.86% of 15m transects, vs. 77.27% of 6m transects; Figure 9).

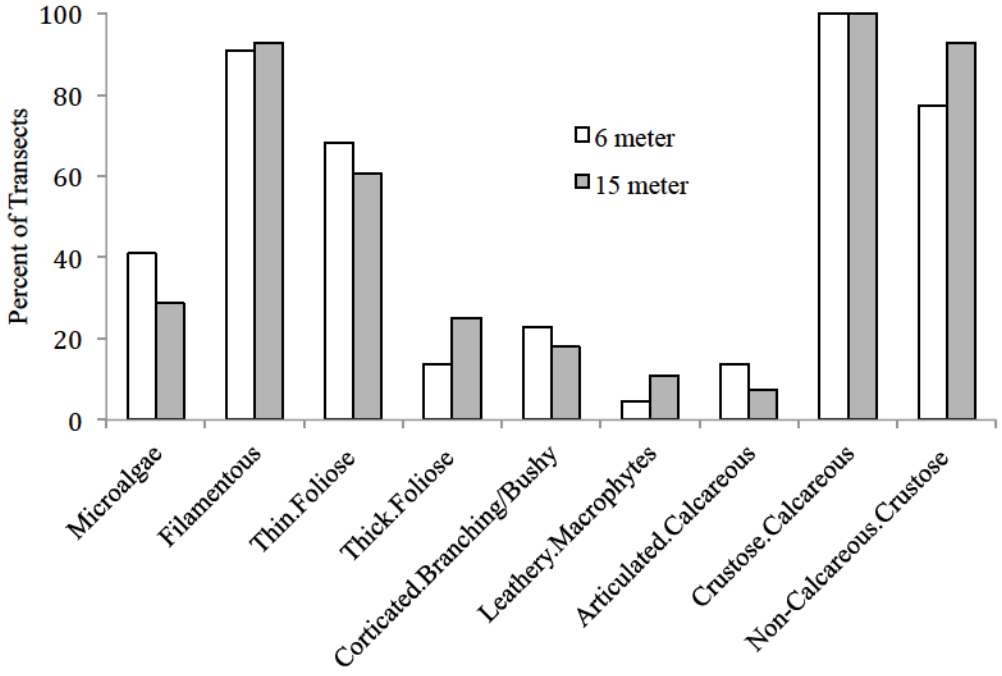

Figure 9: Presence of functional groups by percent of transects at each depth (6 and 15m).

Principal Components Analysis

Principal component loadings for the transect data were similar to those for the site data: 'Calcareous Crustose' loaded positively on PC1, and accounted for 55.60% of total variance. 'Thin Foliose' (+) and Filamentous (-) groups loaded primarily on PC2, and accounted 23.36% of total variance. PC3 and PC4 accounted for 11.64 and 5.89% total variance, respectively (Figure 10).

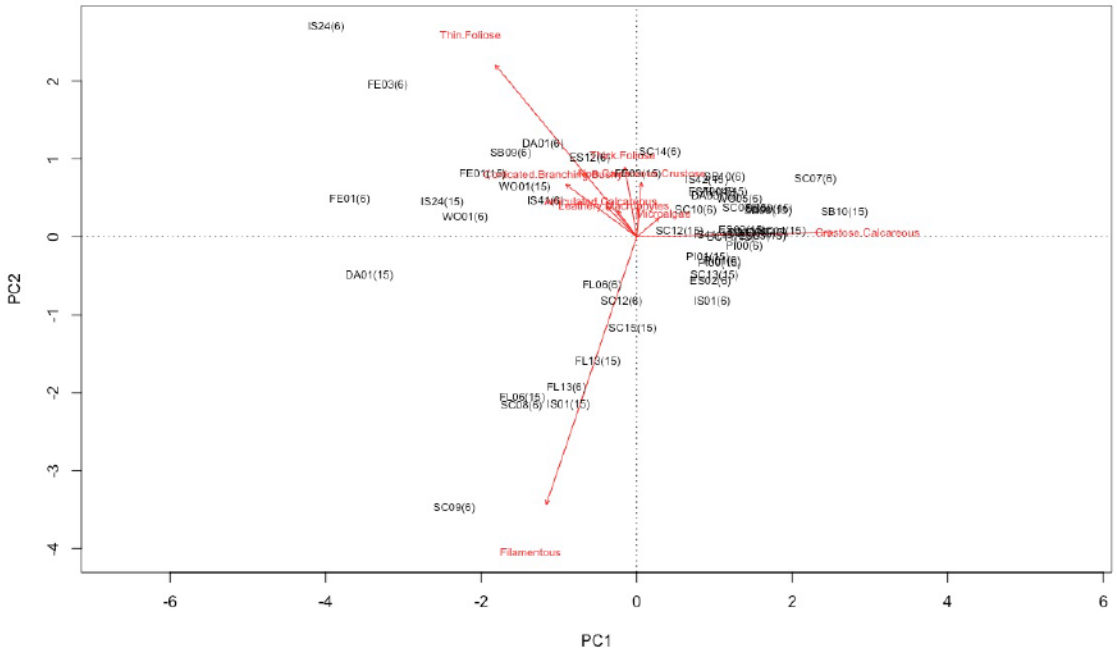

Figure 10: Non-metric PCA plot of macroalgal functional group percent cover data (per transect). Black labels are Transect Codes(depth in meters), red labels are macroalgal functional groups (factors).

Cluster Analysis

2 groups explained 47.99% of variability in the cluster analysis, and was the best-fit model (Figure 11). Further groupings in order of descending percentage (%): 4 groups (47.63), 6 groups (46.99), 5 groups (46.17), 7 groups (44.56), 3 groups (43.80), 8 groups (41.51), 9 groups (41.20), and 10 groups (39.88). Eight transects grouped separately from the rest (Figure 15), and in order of within-group decreasing dissimilarity (increasing similarity) included: 15m at Cabo Douglas (Fernandina, FE01), both 6m transects (equally dissimilar) at Punta Espinosa (Fernandina, FE03) and Caleta Derek (Isabela, IS24), 6m at Cabo Douglas (Fernandina, FE01), 15m at Fondeadero (Darwin, DA01), 6m at Las Tijeras (San Cristobal, SB09), and finally (equally dissimilar) 6m at Corales (Wolf, WO01) and 15m at Caleta Derek (Isabela, IS24).

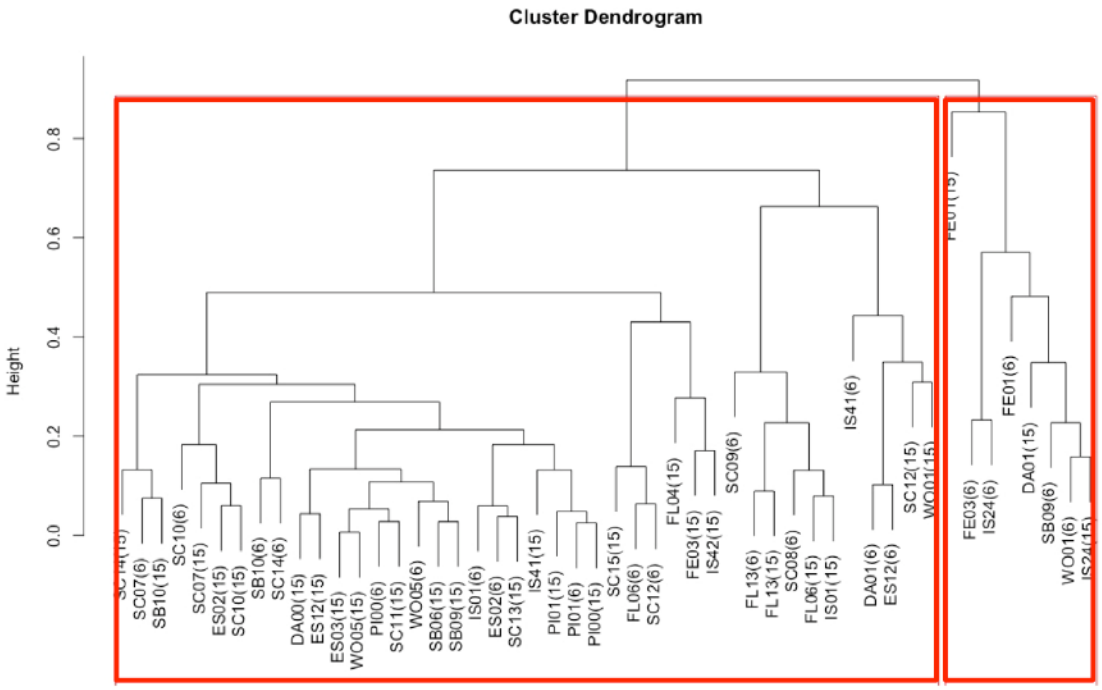

Figure 11: Cluster dendrogram of all transects, with best-fit groups outlined in red. Labels are: Transect Code (depth in meters).

Functional group diversity (# of groups recorded) did not vary significantly with depth (Figure 12).

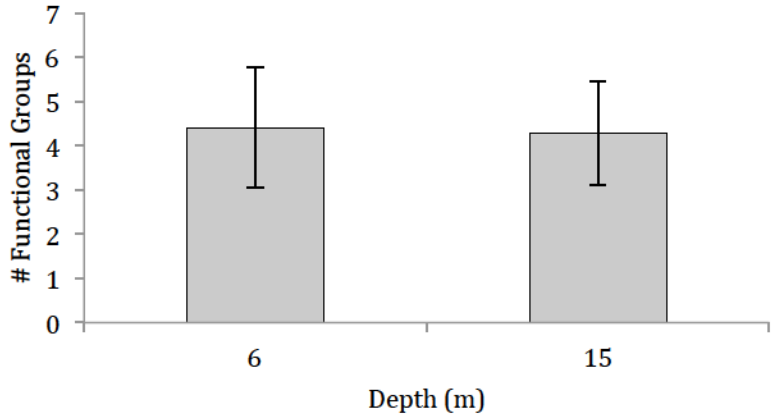

Figure 12: Average number of functional groups per depth. Error bars represent standard deviations.

Functional group diversity did decline with increasing cover of 'Calcareous Crustose' ($p = 0.015$) though with high variability ($R^2 = 0.117$; Figure 13).

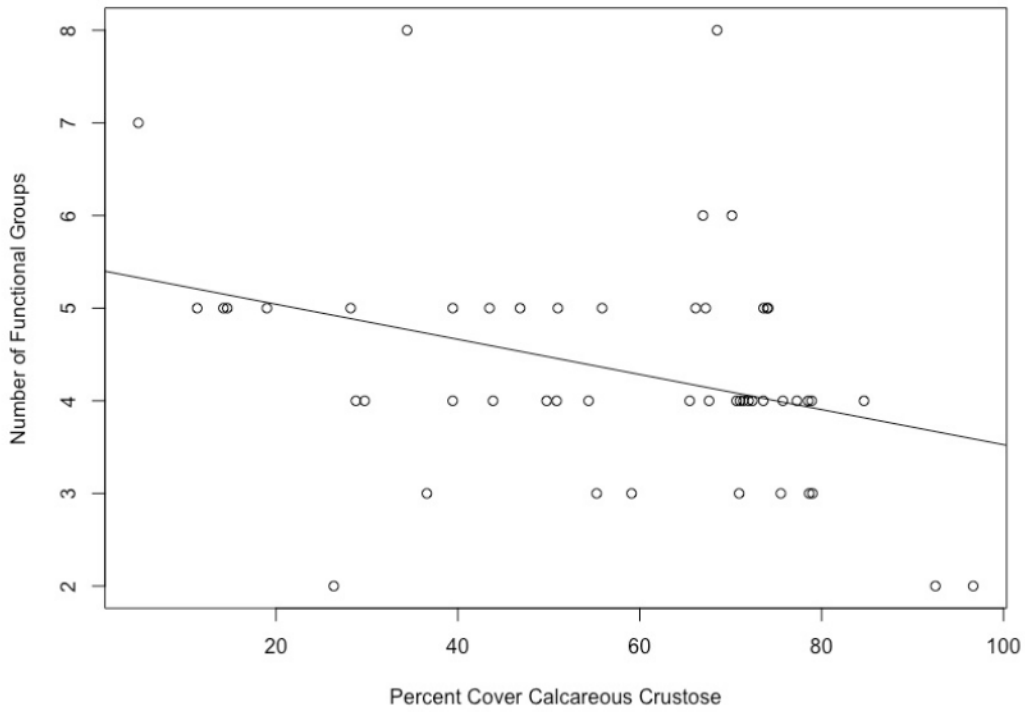

Figure 13: Relationship between # of functional groups recorded per transect, and cover of 'Calcareous Crustose' group.

Sites with High Dissimilarity and/or High Diversity:

Cabo Douglas (FE01)

Eight groups (7 groups in 6m, 5 groups in 15m) were recorded at Cabo Douglas on Fernandina Island (FE01), which only lacked the 'Microalgae' group. On the 6m transect at Cabo Douglas, the lowest overall cover of 'Crustose Calcareous' (4.87%) was recorded out of all transects at all sites. Relatively high cover (36.06%) of 'Corticated Branching/Bushy' was recorded, mainly as *Sargassum* (33.72 % cover, remainder as *Asparagopsis*). Of all transects, this was the second highest cover of this group (after the 15m transect at the same site, see below). Also on the shallow (6m) transect at Cabo Douglas, 30.02% cover of 'Thin Foliose' (all as Ulva), and 22.03% cover of 'Filamentous'(as *Polysiphona* and *Ceramium*) was recorded. All other groups were recorded at <5% cover on this transect. These included 'Non-Calcareous Crustose' (as *Hildenbrandia* and *Ralfsia*) at 4.09%, 'Thick Foliose' (as *Rodymenia* and *Kallymenia*) at 2.34%, and 'Leathery' (as *Spathoglossum*) at 0.58%.

On the 15m transect at Cabo Douglas, the highest (42.69%) cover of 'Corticated Branching/Bushy' was recorded of all transects sruveyed (25.69% *Gelidium*, 13.38%

Asparagopsis, and the remainder as *Prionitis*). 'Non-Calcareous Crustose' covered 21.06% (primarly as *Hildenbrandia* at 20.81%, and the remainder as *Ralfsia*). 'Crustose Calcarous' was recorded at 14.65%, the 4th-lowest of all transects surveyed. This site also yielded 11.46% cover of 'Articulated Calcareous', the highest cover of this group at all transects surveyed. 'Thick Foliose' (as *Rhodymenia*) covered the remaining 9.55%.

Caleta Iguana (IS41)

Eight groups were recorded (in both 6 and 15 meter transects) at Caleta Iguana (Isabela, IS41). The only group not recorded in either transect was 'Articulated Calcareous.' Though it grouped with the majority of sites in the cluster analysis, the 6m transect at Caleta Iguana was the most dissimilar within that group (Figure 15). On that transect, 'Crustose Calcarous' was recorded at 34.41%. 'Thick Foliose' (recorded primarily as *Kallymenia* and *Rhodymenia*) totaled 17.85%. 'Thin Foliose' (as *Ulva*) was recorded at 12.29%. 'Non-calcareous Crustose' consisted of both brown (*Ralfsia*) and red (*Hildenbrandia*) crusts, and totaled 10.88%. Red (*Ceramium* and *Polysiphona*) filaments were recorded at 10.48% total cover. 'Leathery Macrophytes' was recorded as *Spathoglossum*, at 5.69%, the highest cover for this group of all transects surveyed. 'Corticated Branching/Bushy' was recorded as *Gelidium* and *Hypnea*, at 4.52%. 'Microalgae' was recorded as brown mats of chain-forming diatoms, and totaled 3.88%.
In 15m at Caleta Iguana, the situation was much different. 'Crustose Calcarous' dominated at 68.5% cover. Of the remaining seven groups, only three were recorded at >2% cover: 'Red Filament' cover was recorded at 10.25%, 'Thick Foliose' (mostly as *Kallymenia*) at 9.39%, and 'Non-Calcareous Crustose (as *Hildenbrandia, Ralfisa,* and *Codium*) at 7.76%.

The other sites which grouped with Cabo Douglas in the cluster analysis (Figure 9) included Punta Espinosa (FE03), Caleta Derek (IS24), Fondeadero (DA01), and Corales (WO01).

At Punta Espinosa (Fernandina, FE03) 6 total groups (5 at each depth) were recorded. On the 6m transect, cover was recorded as such: 'Thin Foliose' (as *Ulva*) at 55%, 'Crustose Calcareous' at 19%, 'Corticated Branching/Bushy' (as *Hypnea*) at 11%, 'Filamentous' (as *Polysiphona* and *Ceramium*) at 8% and 'Thick Foliose' (as *Padina* and *Dictyota*) at 7%.

At 15m, cover was recorded as 'Crustose Calcareous' at 51%, 'Corticated Branching Bushy' (as *Asparagopsis* at 12% and *Gelidium* at 8%) at 20%, 'Thick Foliose" (as *Kallymenia, Dictyota,* and *Padina*) at 16%, 'Non-Calcareous Crustose' (as *Hildenbrandia*) at 9%, and 'Thin Foliose (as *Ulva*) at 4%.

At Caleta Derek (Isabela, IS24) 6 total groups were recorded (5 groups at 6m, 4 groups at 15m). On the 6m transects, the highest cover of 'Thin Foliose' (77.71%, all as

Ulva) was recorded out of all transects surveyed. The reminder of cover was 'Crustose Calcareous' at 14.23%, 'Filamentous' (as *Polysiphona* and *Ceramium*) at 6.86%, 'Corticated Branching/Bushy' (at *Laurencia*) at 0.63%, and 'Non-Calcareous Crustose' (as *Hildenbrandia*) at 0.57%.

At 15m, cover was recorded as 'Thin Foliose' (as Ulva) at 41.77%, 'Crustose Calcareous' at 29.75%, 'Filamentous' (as *Polysiphona* and *Ceramium*) at 26.58%, and 'Microalgae' (as brown chain-forming diatom) at 1.9%.

At Fondeadero (Darwin, DA01), a total of 5 groups were recorded (5 on each transect). In 6m, 'Crustose Calcareous' was recorded at 43.48% cover, 'Thin Foliose" (as *Dictyota grossendentata(?)*) at 33.41%, 'Non-Calcareous Crustose' (as *Lobophora, Ralfsia, and Peysonnelia*) at 13.96%, 'Filamentous' (as both green and red filaments) at 8.70%, and 'Microalgae' (as *Lyngyba*) 0.46%.

In 15m, 'Filamentous' (as both green and red filaments) was recorded at 39.27%, 'Thin Foliose" (as *Dictyota grossendentata(?)*) at 32.39%, 'Non-Calcareous Crustose' (as *Lobophora, Ralfsia, and Peysonnelia*) at 12.96%, 'Crustose Calcareous' at 11.34%, and 'Microalgae' (as Lyngyba) at 4.05%.

At Corales (Wolf, WO01), a total of 5 groups were recorded (5 in 6m and 4 in 15m). In 6m, 'Thin Foliose' was recorded (as *Dictyota grossendentata(?)*) at 30.20% cover, 'Crustose Calcareous' at 28.22%, 'Filamentous' at 24.27% (as *Polysiphona* and *Ceramium* at 23.29%, and green filament at 0.99%), and 'Microalgae' (as Lyngyba) at 1.46%.

In 15m, Non-Calcareous Crustose' (as *Peysonnelia*) was recorded at 47.73% cover, 'Crustose Calcareous' at 28.79%, 'Thin Foliose' (as *Dictyota grossendentata(?)*) at 13.37%, and 'Filamentous' at 9.85% (as *Polysiphona* and *Ceramium* at 8.33%, and green filament at 1.55%).

Sites with Low Dissimilarity and/or Low Diversity:

25 sites grouped together, characterized by high 'Crustose Calcareous' cover, low diversity and low dissimilarity. Exemplary sites from this group include Canal Itabaca (Santa Cruz, SC09), Manzanillo (San Cristobal, SC10), Bajo Gardner (Espanola, ES03), El Eden (Santa Cruz, SC07), and (Pinta, PI01)

At Canal Itabaca 2 (Santa Cruz, SC09), data was only recorded at 6m due to bathymetric heterogeneity of the site (flat bottom, very little slope). Only 2 groups were recorded: 'Filamentous' at 73.64% cover (as 43.93% red filaments and 23.66% green filaments), and 'Crustose Calcareous' at 26.36%.

At Manzanillo (San Cristobal, SB10) 4 groups were recorded in total, 4 in 6m and 2 in 15m. Overall (pooled transect data) cover of 'Calcareous Crustose' was 86.98%, the highest of all sites.

In 6m, 'Crustose Calcareous' was recorded at 77.28% cover, 'Thin Foliose' at 16.69%, 'Filamentous' at 5.25%, and 'Non-Calcareous Crustose' at 0.78%.
In 15m, 'Crustose Calcareous' was recorded at 96.67% cover, and 'Filamentous' at 3.33%.

At Bajo Gardner (Espanola, ES03), data was only recorded in 15m due to high current and surge in shallower water. Three groups were recorded in total; 'Crustose Calcareous' at 78.99%, Non- Crustose Calcareous' at 11.16%, and 'Filamentous' at 9.85%.

At El Eden, (Santa Cruz, SC07) high overall cover of 'Crustose Calcareous' was recorded (83.07%). Five groups were recorded at the site (2 in 6m and 5 in 15m).
In 6m, 'Crustose Calcareous' was recorded at 92.51, the second highest cover of this group across all transects surveyed. The remaining 7.49% was covered by 'Thin Foliose' (recorded as *Ulva*).

In 15m, 'Crustose Calcareous' was recorded at 73.62% cover, "Microalgae' (as brown diatom mat) at 11.08%, 'Non-Calcareous Crustose' (as *Lobophora* at 1.53%, *Ralfsia* at 0.42%), and 'Filamentous' at 3.94%.

At Turismo (Pinta, PI01), 4 groups were recorded at the site, and 4 in both 6m and 15m.
In 6m, 'Crustose Calcareous' was recorded at 71.39% cover, 'Filamentous' at 15.97% (as 8.06% green, remainder as reds), 'Non-Calcareous Crustose' at 10.56% (as *Peysonellia* and *Hildenbrandia*), and "Microalgae' (as brown diatom mat) at 2.08%.

In 15m, 'Crustose Calcareous' was recorded at 67.62% cover, 'Non-Calcareous Crustose' (as *Peysonellia* and *Hildenbrandia*) at 15.41%, 'Filamentous' at 15.26% (as green filaments at 13.98%, remainder as reds), and "Microalgae' (as brown diatom mat) at 1.71%.

DISCUSSION

Functional Group Approach:

The functional group approach is a useful tool for studying variation in ecosystem-level functioning of macroalgal communities in the Galapagos. Since the functional group scheme used here has been established as a viable means of grouping species of similar productivities (Littler, 1980; Steneck & Dethier, 1994; Padilla & Allen, 2000), the differences in community composition will ultimately be useful in estimating

variation in macroalgal community production across depths, sites, and regions in the Galapagos Archipelago, and thus inform management of the Galapagos Marine Reserve. Further, a mechanistic understanding of how oceanographic variation, consumer pressures, and human activities can influence patterns in the functional diversity of macroalgal communities would ultimately be important when making predictions of future changes.

While the functional group approach used here did allow for comparisons of community structure across sites and between the depths surveyed, the methods lead to several limitations in both analysis and interpretation of the data. One clear example is the inclusion of both *Ulva* and *Dictyota grossedentata* in the "Thin Foliose" group. *Ulva* was mostly encountered in West and South/central vs. *D. grossedentata* in North. Similarly, 'Non-Calcareous Crustose' was primarly recorded as either *Lobophora, Ralfsia,* or *Hildenbrandia,* and *Peyssonellia*. Therefore this approach offers diminished power in determining species-level dissimilarity between transects or sites compared to, for example, Schils and Coppejans (2003) assessment of biogeographic affinities of macroalgal communities in the upwelling influenced Socotra Archilepago in the Indian Ocean. In that work more effort was made to identify species, and though results were based on macroalgal biomass and not cover, regional dissimilarities in community compositions were more apparent.

The functional group approach also negates the ability to examine taxonomic or phylogenetic diversity, as species from distant lineages would group together. For example, the 'Filamentous" group encompasses species from all three major macroalgal phyla (Rhodophyta, Chlorophyta, and Ochrophyta, Appendix II). In fact, 'Crustose Calcareous' was the only group in which taxonomic diversity was low, containing only species from the sub-class Corallinophycidae (Rhodophyta). Therefore "functional diversity" should not be in any way substituted or misinterpreted as taxonomic diversity.

General Trends in Sites and Transects:

Dissimilarity across sites and transects was primarily due to variability in cover of the 'Crustose Calcareous' group, and secondarily to variation in cover of the 'Filamentous' and 'Thin Foliose' groups. Because of the primary influence of 'Crustose Calcareous', sites with the lowest cover that functional group were the most dissimilar, and grouped separately from the other sites. All other groups were generally of lesser influence in determining dissimilarity, though were important for determining differences based on diversity.

Based on the results of this work, we propose a three-region scheme based on dissimilarity in macroalgal functional groups between sites: West, North, and Central/South. Virtually the entire Central/South region, and several sites in other regions (Bahia Urvina, Isabela, IS42; Fondeadero, Wolf, WO05) were dominated by the 'Crustose Calcareous' group, while the most diverse or dissimilar sites with the lowest

cover of 'Calcareous Crustose' were located in the West and North regions of the archipelago. The group 'Leathery Macrophyes,' which includes some of the physically largest and most structurally complex of all macroalgal species in Galapagos, was limited to sites in the West (IS41, IS42, FE01), as was the 'Corticated Branching/Bushy' group (particularly in both transects at Cabo Douglas).

The dissimilarity of the most diverse or unique sites, such as Cabo Douglas, was driven partly by low cover of 'Crustose Calcareous,' but also by higher cover of the "Corticated Branching/Bushy" and "Articulated Coralline" groups. This was one of the only sites where *Sargassum* was recorded in any abundance (up to 78% cover in one quadrat). At other sites, dense patches of *Sargassum* were noted in shallow (< 5m) benthos, but not recorded in transects. On the 15 m transect at Cabo Douglas, 11.46% cover of 'Articulated Calcareous' was recorded, a degree of magnitude more than at Arricife (Darwin, DA00; 1.36%), where the next highest cover of this group was recorded. Cabo Douglas was the westernmost site surveyed, and the closest to the ECC upwelling center.

In the western region, an abundance of large macroalgae were found, comprising several genera mostly from Rhodopyta and Ochrophyta. Besides *Sargassum,* commonly abundant genera included *Spathoglossum*, *Kallymenia*, *Hypnea*, and *Plocamium*. These leathery, bushy, and foliose macroalgae offer abundant habitat for fish, benthic invertebrates, and encrusting organisms. This is the only region where which algae commonly provide large, three-dimensional substrate, and where kelp forests have been reported (Graham et al. 2007). Elsewhere in the archipelago, habitat-seeking animals may rely on benthic encrusting invertebrates such as corals and sponges, or the heterogeneity of the rocky reef itself. We would thus expect the Western region fauna to be more heavily dependent on macroalgal abundance for habitat, and thus most susceptible to losses in macroalgal cover due to for instance El Niño events or over-grazing by herbivores.

In temperate waters, high benthic cover of crustose coralline algae on shallow reefs is often associated with urchin "barrens;" areas that have been perpetually overgrazed by high densities of urchins, leaving behind only bare rock or a thin veneer of crustose coralline algae (Ling et al. 2014). Over the last three decades, urchin barrens have been reported as increasing in frequency and persistence in the Galapagos, (Kendrick, 1988; Edgar et al. 2010; Sonnenhozer et al. 2009) apparently mainly due to overfishing of urchin predators, though it is unclear how recruitment dynamics may also influence their populations.

Urchin densities in Galapagos have been reported to peak between 5 and 12m depth (Witman & Dayton, 2001), and observations during this work included high densities (>50/m^2) of urchins on deeper transects (mainly *Eucidaris* in the South/Central and *Lytechinus* in the West), and of variable urchin distributions and grazing behavior between depth strata (less abundant and more cryptic in shallow, and exposed and

actively grazing in deep). Experiments in Galapagos have shown that these urchin behavioral patterns may be predator-avoidance strategies (Dee et al., 2012). Studies elsewhere point to wave energy as a driving factor in similar urchin behavior (ref). The urchin barren situation in Galapagos is in no way unique. Urchins, via grazing, are known to be highly influential in structuring benthic communities globally (Steneck, 2013). At sites across the Canary Islands (another tropical upwelling-influenced archipelago) locally high urchin densities have been correlated with lack of urchin predators, physically complex substrate, and reduced cover of fleshy macroalgae (Tuya et al., 2004).

Exceptions to this general pattern of 'Calcareous Crustose' dominance occurred in the West and North, but also in South/Central sites where 'Filamentous' and 'Thin Foliose' groups were recorded in abundance (Las Tijeras, Punta Estrada). The locally high cover of 'Filamentous' could be directly attributed to algal "farming" by damselfish (particularly in shallower depths). Aggressive territorial behavior can limit urchin grazing and indirectly facilitate algal growth (Irving & Witman, 2009), and selective "farming" can directly influence algal community composition (Sammarco, 1983). Thus filamentous and thin foliose algal group cover may be directly related to the distribution of damselfish populations, and less closely influenced by regional oceanography.

Damselfish activity is one explanation for the higher cover of 'Thin Foliose' algae on shallow transects. However, hydraulic energy, sedimentation, sand scour, and light could also be playing a role. Higher hydraulic energies in shallow water (i.e. wave surge) can limit grazing by urchins and therefore indirectly facilitate algal growth (Lauzon-Guay & Scheibling, 2007). Deeper transects were often close to the sediment-rock interface, and sand scour can limit algal growth, potentially influencing any depth-related patterns (Kendrick, 1991). Algae are photosynthetic and light energy is most intense at the oceans' surface but dissipates rapidly with depth. Highly stressful intertidal conditions (light, temperature, and salinity) exist in Galapagos, and could explain the disappearance of *Blossivellia* (Kendrick, 1988). Deeper distributional boundaries are much more difficult to measure, and remain largely unstudied in Galapagos (Tompkins & Wolff, 2017). However, most macroalgal growth is ultimately restricted to the first 100m of the water column, with light-influenced zonation patters apparent across depths (Saffo, 1987). In all likelihood, a combination of these factors at varying scales and intensities is driving the measured differences in cover of macroalgal functional groups between depths and sites.

The 'Filametous' and 'Thin Foliose' algal groups are the 2nd and 3rd most productive (carbon fixed/biomass/time) of all macroalgal functional groups, respectively (Littler & Murray, 1974; Littler, 1980; Chapter 3). Therefore the depth-related variation in cover of these groups could result in less overall macroalgal production in deeper waters. Because the macroalgal species functional groupings are based on gross morphology, regional variation in cover of macroalgal functional groups in the Galapagos could therefore greatly influence patterns in overall macroalgal standing stocks and

benthic productivity across the archipelago. Ultimately, the results of this work will be used as a foundation for quantifying regional-scale differences in macroalgal community productivity, biomass, and habitat provisioning. In addition, the information presented here can serve as a baseline for quantifying future changes in the ecological function of macroalgal communities across the GMR.

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Chapter 3: Production and biomass of macroalgal communities across the Galapagos archipelago during ENSO-neutral conditions.

Abstract: Marine ecological models are increasingly being used in ecosystem-based fisheries management, and their power to predict changes in energy flows through trophic webs depends on accurate parameterization. On hard shallow benthos, macroalgal community (MaC) primary production supports diverse and abundant coastal marine ecosystems, and and may be particularly important for supporting life on upwelling-influenced coasts in the tropics such as the Galapagos Islands, were macroalgal herbivores are abundant. Different trophic models have been created for subsystems of the Galapagos Marine Reserve, and show regional variation in their estimates of MaC Biomass (B; West > South/Central > North) and Production/Biomass (P/B; West = North > South/Central). To determine if these differences are due to either natural variability or sampling error, MaC B and P values based on community composition and overall MaC cover per site were calculated for 6 and 15 meter depths. After scaling to overall percent cover of macroalge, these parameter estimates varied greatly across transects and with depth. Across the archipelago, B (tons/km^2) ranged from 56.30, 1348, and P (tons/km^2/yr) ranged from 187.30 to 13036.63. Mean MaC production was higher in 6m than in 15m. An exclusion study showed MaC production in the absence of herbivores to be greater in 6m than in 15m.

Keywords: Macroalgae, ecological modeling, Galapagos, macroalgal biomass, primary production, ecotrophic parameters

INTRODUCTION

Marine ecological models are increasingly being used in ecosystem-based fisheries management (Pikitch et al., 2004; Hillborn, 2011) and to predict system behavior as driven by climate variability or global change. A realistic design – and accurate parameterization of these models – is essential to making truthful ecological predictions upon which marine resource management can then be based. Out of a great number of modeling approaches, trophic energy flow models have been used frequently for these purposes (Pauly et al., 2000).

For each compartment or functional group these models require input parameters such as biomass, production and consumption rate. These parameters are either measured directly or indirectly, or when unavailable, may be estimated by the model itself (Christensen & Walters, 2004). Primary productivity parameters (for phytoplankton, macroalgae, etc.) are often only indirectly estimated (e.g. from remote sensing information), despite the fundamental importance of marine primary producers, which provide direct sustenance to the majority of life in the sea and form the base of marine trophic webs. Macroalgal (seaweeds, or algae visible to the naked eye) photosynthesis provides an important source of primary production in coastal marine ecosystems (Mann, 1973). Their abundance and diversity is known to vary with latitude, being generally lower in tropical waters than in temperate or even polar marine ecosystems (Kerswell, 2006). Therefore macroalgal communities (MaC) are generally not considered to contribute significantly to overall system productivity in the tropics (Ramus, 1992).

However, exceptions to this general rule can be found in tropical upwelling systems, where colder, nutrient-rich deep water is forced towards the ocean's surface, displacing otherwise warm and nutrient poor waters. Tropical upwelling regions include the lower latitude portions of the Humboldt (Southern East Pacific) and Benguela (Southern East Atlantic) current systems; The Northwestern Indian Ocean (at the mouth of the Gulf of Aden); Western and Southern India; Northwestern Australia; Southeast Brazil, the Pacific coasts of Nicaragua and Costa Rica, and the Galapagos Islands. In some of these regions, Macroalgae have been reported in great abundance, and MaC production has been highlighted as a structuring factor in nearshore tropical marine food webs (e.g. Ruiz & Wolff, 2011).

As with other primary producers, macroalgal photosynthetic rates and growth performance vary with changes in ambient photons (light), temperature, and chemistry (nutrients, pH), and fluxes in these factors will influence the quantity and quality of primary production available to the food web (Steele, 1962; Bunt, 1975; Gattuso et al., 2006). An extreme example would be the influence of ENSO cycles on the marine productivity of tropical upwelling regions. During strong "El Niño" events, trade winds

greatly decrease in the Eastern Pacific, sea surface temperatures rise due to the cessation of upwelling of cold nutrient enriched subsurface waters, and dissolved nutrient contents decline. As a consequence, overall marine primary production decreases dramatically during El Niño (Pennington et al., 2006).

The equatorial Galapagos Islands are located at the northern extreme of the Humboldt Current Upwelling System, and at the western margin of the Equatorial Under Current (EUC), which upwells to the surface just west of the archipelago (Chavez & Brusca, 1991). Compared to continental coastlines at the same latitude, the marine ecosystem of the Galapagos is therefore more productive and diverse (Pennington et al., 2006). Here, macroalgae has been reported as abundant, and of great importance in the marine trophic web of the archipelago (Okey et al., 2004; Ruiz & Wolff, 2011). It has also been shown that these MaC are ecologically responsive to both top-down and bottom-up influences (Vinueza et al., 2006).

The Galapagos Marine Reserve (GMR), which was created in 1998 to ban the industrial fishery from the archipelago and to define zones of different use, is of great value both to science and society. While the ban of the industrial fishery was successful, an active artisanal fishery still exists in the islands. This fishery has experienced both overexploitation in some areas of vulnerable invertebrate stocks (such as lobsters and sea cucumbers), as well as ENSO-related catch declines (Edgar et al., 2010).

To improve our understanding of the interaction between this fishery and the ecosystems in the region, small-scale trophic models have been created in three different biogeographic regions of the archipelago to allow for predictions of changes in system configuration and energy flow pathways in response to fluctuating physical and biological variables (Okey et al., 2004; Ruiz & Wolff, 2011; Ruiz et al., 2016). These studies offer quantitative estimates of compartment biomasses and production, and determined the trophic influence of macroalgae in their respective systems (Table 1).

Table 1. Galapagos marine ecosystem model results. MB = Macroalgal Biomass (tons/km^2); P = Production (tons km^{-2}/yr); SB= System Biomass (tons/km^2)

Ref.	Region	Location	MB	% SB	P	P/MB	Trophic Impact
Okey et al. 2004	Central /South	North Shore of Floreana	256.80	9.8	3074.6	12.00	5th highest indicated interaction strength
Ruiz and Wolff 2011	West	Bolivar Channel	800.475	44.6	12543.44	15.670	3rd highest relative total impact
Ruiz et al. 2016	North	Darwin and Wolf	76.480	8.149	1199.74	15.687	3rd highest (Net impact)

For all these models, macroalgae were of the top five most influential functional groups. Interestingly, the sub-region models exhibit large disparities in estimates of standing stocks and production of macroalgae. There are several potentially responsible factors driving this difference, including sampling error and intrinsic marine

environmental and biological gradients between regions. In all cases, production and mortality of the macroalgal functional group was determined from literature sources, while biomass was directly measured or estimated in field surveys.

Results of these reported models suggest regional macroalgae biomass differences, but these values may have resulted (at least in part) from different methodologies used. Okey et al. (2004) "estimated biomass based on measured standing wet biomass at two sites on Santa Cruz Island, and based on subtidal observations." Ruiz and Wolff (2011) based their estimates on "measured standing wet biomass at two low intertidal sites on Fernandina Island, and based on subtidal observations during the Subtidal Ecological Monitoring (SEM)". Ruiz et al. (2016) derived estimates "based on underwater observations during the underwater surveys that the Charles Darwin Foundation (CDF) has carried out each year at 5 sites in Darwin and 6 sites in Wolf, between the years 2004 and 2008."

In spite of these differences in methodologies, both the information reviewed by Tompkins and Wolff (2017) and the variability in MaC composition described previously (Chapter 2) indicate that geographic variation in MaC composition across the archipelago is the cause of sub-region differences in biomass and productivity. Both of these parameters are influenced by algal morphology and vary greatly between functional groups and between intra-specific morphologies (Littler, 1980; Steneck & Dethier, 1994; Padilla & Allen, 2000). Generally, thin foliose forms are much more productive than coarsely branching forms, which are more productive than calcareous crustose forms. Overall, production per biomass of MaCs is therefore directly linked to functional group composition, which varies across the Galapagos Archipelago (Chapter 2).

Integration of larger scale knowledge of ecological patterns and processes is necessary to improve predictive power at the level of the entire Galapagos Marine Reserve. In particular, variability in macroalgal biomass and productivity across the archipelago could have an important role in structuring marine communities and influencing energy flows through the food web. Therefore this work seeks to produce improved (baseline) estimates of MaC parameters (biomass and production) of the Galapagos archipelago, and characterize the ENSO conditions during sampling.

In order to address and critically analyze the differences in published production and biomass values, we intend to quantify variation across sites and transects by 1) quantifying the overall cover of MaCs at all transects surveyed (vs. sand and sessile invertebrates); 2) estimating the overall standing stocks of MaC (biomass in tons/km^2); and 3) estimating actual MaC production (tons/km^2/year) from biomass and Production/Biomass values. Since the previous ecological models' data (at all trophic levels) was taken from the CDF Ecological monitoring program, and was collected at both 6 and 15m depths, this work will also seek to compare MaC parameters between these depths, and use an in-situ macrograzer exclusion study to directly measure production at both depths.

Cover of the "Calcareous Crustose" functional group was previously determined to be a dominant component of the MaCs in the Galapagos, and a driver of dissimilarity between sites and transects. Here we will also test the relationship between cover of all individual functional groups and overall MaC production, to determine which groups are most influential in determining overall benthic community primary production.

Since ENSO cycles are clearly important drivers of macroalgal production and community composition in the Galapagos (Vinueza et al., 2006; Tompkins & Wolff, 2017), it was crucial to characterize the ENSO conditions over the sampling period.

METHODS

Proportion of MaC cover:

See Chapter 2 for survey methodology. To correct for transect-related variability in overall MaC cover (i.e. at many sites <100% macroalgal cover was recorded), any non-algal (sand, bare rock, sessile invertebrate, etc.) data points were retained and used to determine actual % cover of MaC at each site.

Biomass estimation:

Since directly removing and measuring all macroalgal standing stock was not feasible, an estimation method was designed based on sub-sampling and extrapolation, or use of literature values when needed. Direct measurements were taken of available groups in the field. This was done whenever possible, and when time and/or logistics allowed during both survey and experimental work. However, most samples were taken during experimental work at Isla Caamaño, Santa Cruz Island (SC12, Chapter 2).

To collect as few as possible functional groups per sample, and minimize disturbance to the marine reserve, replicate $10cm^2$ scrapings of subtidal (substrates between 4 and 16m depth) macroalgae were collected between May and August of 2014 using a metal spatula and a manual slurp sampler (modified from Chatzigeorgiou et al., 2012), which pumped scrapings into 1 liter, 60um mesh size collection bags. Samples were transported to the CDF BIOMAR laboratories, rinsed and/or picked clean with forceps of infauna and epiphytes, patted dry, and weighed to the nearest 0.01g with a Mettler Toledo MonoBloc electronic scale, and averaged to produce a biomass per functional group value (B_{fg}). For any missing groups, or groups with unacceptably low sample sizes, literature values were supplemented. Literature values were most often reported as dry weights, so conversion factors were applied, as per reported moisture contents of different functional groups.

B_{fg}'s were then scaled to the % cover of each functional group at each transect, and these values summed and multiplied by the proportion of macroalgal community cover at each transect to calculate the macroalgal biomass per transect (MaCB in $tons/km^2$).

Production derived from in-situ experiments and the literature:

To identify variation in productivity of macroalgal communities in Galapagos, an overall production value (P_{fg}) was created for each functional group. P_{fg} is based on actual production data directly measured for one functional group ('Filamentous'), scaled to create relative production values (RPV) for all other groups.

Directly measuring production of filamentous algae was accomplished by "seeding" multiple (25) 100cm^2 un-glazed ceramic tiles. Tiles were fixed to the seafloor amidst patches of filamentous macroalgae (often damselfish nests) until sufficient algal growth was noted. Tiles were then transported to the laboratory, cleaned of any undesirable species and sediments, and their initial wet weights recorded. Tiles were then cultured in semi-controlled conditions (1m x 1m x 1.5m cement basins filled and flushed daily with seawater from adjacent tidal embayment), and weighed daily for a three-week period while ensuring that growth was limited to the 100cm^2 tile area. Change in wet weight over time was averaged for all tiles and scaled to tons/km^2/yr to produce a production value (P_{fg}) for the 'Filamentous' functional group.

The production directly measured for the 'Filamentous' group was used as a baseline ($SF_{filamentous}$= 1), and scaling factors (SF_{fg}) for other groups were based on published production values for other functional groups (Littler & Murray 1974; Littler, 1980; Steneck & Deither, 1994). P_{fg} therefore equals SF_{fg} multiplied by the production value directly measured for the 'Filamentous' group. Macroalgal community production per transect (MaCP) was then calculated by multiplying P_{fg} by the percent cover of each functional group, summing the production values for all groups present per transect, and multiplying the result by the proportion of macroalgal community cover of each transect.

Production/Biomass ratio (P/B):

P/B was calculated for all macroalgal functional groups by dividing P_{fg} by B_{fg}, and for all transects surveyed by dividing MaCB/MaCP per transect.

In situ study at two depth strata:

To test for differences in estimated MaC biomass, production, and P/B across the depth strata surveyed (6 and 15m depths) mean parameter values per strata were compared with independent T-tests.

A manipulative experiment was run in an attempt to re-create this difference in-situ at one site. The north-facing coastline of Caamano Island (-0.7587N, -90.2796W) was chosen as the experimental site, due to logistically easier access to the depths required (all other nearby sites <10m max depth). The north side of Caamano offered an 'intermediate' disturbance, neither well protected from or extremely exposed to the predominant winds and swell. At each of 6 and 15 meter depths, five 1m diameter by 25cm height plastic-coated wire mesh cages were bolted to the seafloor. 3cm mesh size was chosen to maximize light and water flow while minimizing biofouling and excluding

the most common macroherbivores at the site, which included large (3-8cm test diameter) *Eucidaris* urchins, and Labrid (parrotfish), Scarid (surgeonfish), Girrelid (chub) and Pomacentrid (damselfish) fishes. Initial biomass (T_0) of macroalgae was determined by scraping replicate 10cm^2 areas of substrate both within and outside (controls) of cages, and recording wet weight of both total scrapings and that of different fuctional groups present within scrapings. This procedure was repeated once a week for five weeks. Whenever possible during this time, transect data was collected using the methods described in chapter 2.

Functional Group Influence on Parameters:

To examine the relationship between cover of individual functional groups and P/B, linear regressions of P/B vs. % cover was run for both site and transect data for all functional groups.

Regional Parameter Variance:

Variability in means (across transects) of each parameter (Biomass, Production, and P/B) per MaC region (North, Central/South, and West, as defined in Chapter 2) were analyzed with one-factor ANOVAs, and any significant (alpha = 0.05) differences identified with post-hoc Tukey HSD tests.

ENSO phase charaterization (MEI Index):

NOAA monitors ENSO conditions by using a Multivariate ENSO Index (MEI; https://www.esrl.noaa.gov/psd/enso/mei/). MEI is based on the six main observed variables over the tropical Pacific: sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky. The MEI is computed separately for each of twelve sliding bi-monthly seasons (Dec/Jan, Jan/Feb,..., Nov/Dec). In order to keep the MEI comparable, all seasonal values are standardized with respect to each season and to the 1950-93 reference period. To determine the ENSO phase, MEI data was extracted from NOAA (https://www.esrl.noaa.gov/psd/enso/mei/table.html), and averaged over the sampling period. Rank MEI scores (https://www.esrl.noaa.gov/psd/enso/mei/rank.html) were also averaged over the sampling period.

Data analysis:

All visualizations and statistical analyses were performed using R. All means are reported +/- Standard Deviations (SD), unless otherwise noted.

RESULTS

Proportion of Macroalgal Community cover:

The cover of MaC per transect ranged from 14.21% (Corales, Wolf Island, WO01), to 100% (at 13 total transects; Figure 1). MaC % cover was higher (t = 2.6044, df = 38.946, p-value = 0.01296) at 6m (89.79 +/- 10.92) than at 15m (76.18 +/- 24.76). Sand cover was higher at 15m (15.36 +/- 20.24) than at 6m (7.65 +/-9.74), as was sessile invertebrate cover (8.46 +/-18.53 at 15m vs. 2.56 +/- 6.02 at 6m).

Figure 1. Benthic cover component proportions (MaC, Sessile invertebrates, and Sand) per transect. Where circles are stacked vertically, transects were performed at both depths, with 6m charts above 15m charts.

Biomass:

Biomass (tons/km^2) estimates per functional group (B_{fg}) ranged from 250 ('Crustose Calcareous') to 4240 ('Leathery'; Figure 2, Table 2). These values were used to determine MaC biomass per transect.

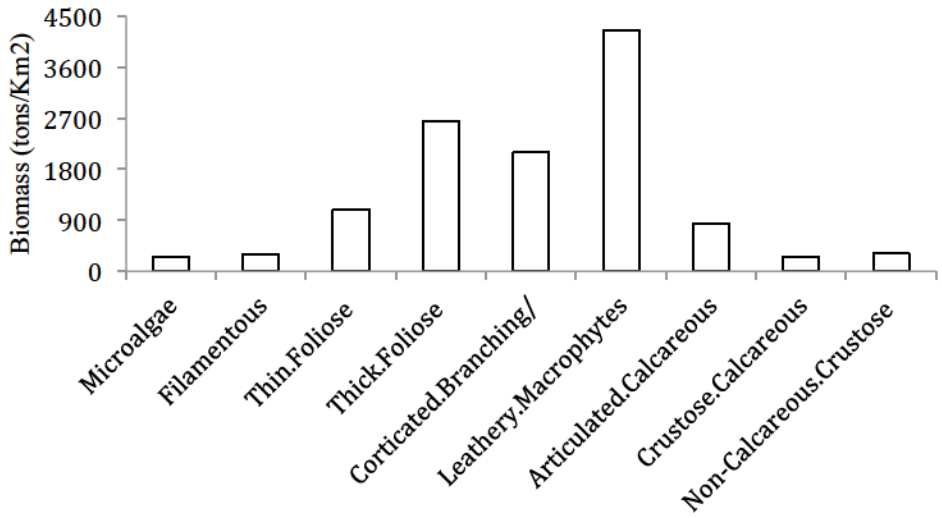

Figure 2: Biomass values used per functional group (B_{fg}).

MaC biomass (tons/km^2) per transect ranged from 56.30 in 15m at (Wolf, WO01) to 1348 in 15m at Cabo Douglas (Fernandina, FE01; Figure 3). Biomass averaged 464.10 +/- 311.96 in 6m, and 337.69 +/-291.31 in 15m ($t = 1.4641$, $df = 43.684$, p-value = 0.1503).

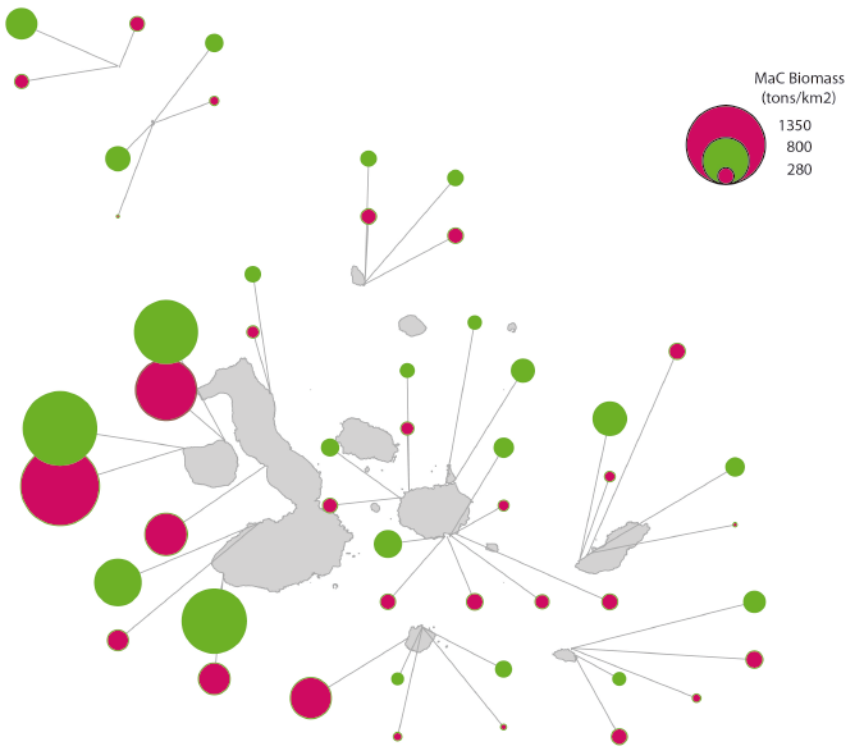

Figure 3: Biomass per transect, circle sizes are relative to biomass values in tons/km2. Where circles are stacked vertically, transects were performed at both depths, with 6m biomass values (in green) above 15m biomass values (in red).

Production:

The average production (tons/year/km^2) of filamentous algae from the in-vitro growth study was 14184.3056. Therefore $P_{fg} = RPV_{fg}$ x 14184.3056 (Table 2). Production per functional groups ranged from 27949.38 for 'Microalgae' to 157.22 for 'Crustose Calcareous' (Table 2). MaC production (tons/km^2/yr) per transect ranged from 187.30 in 15m at (SB10) to 13036.63 in 6m at Caleta Derek (Isabela, IS24; Figure 4).

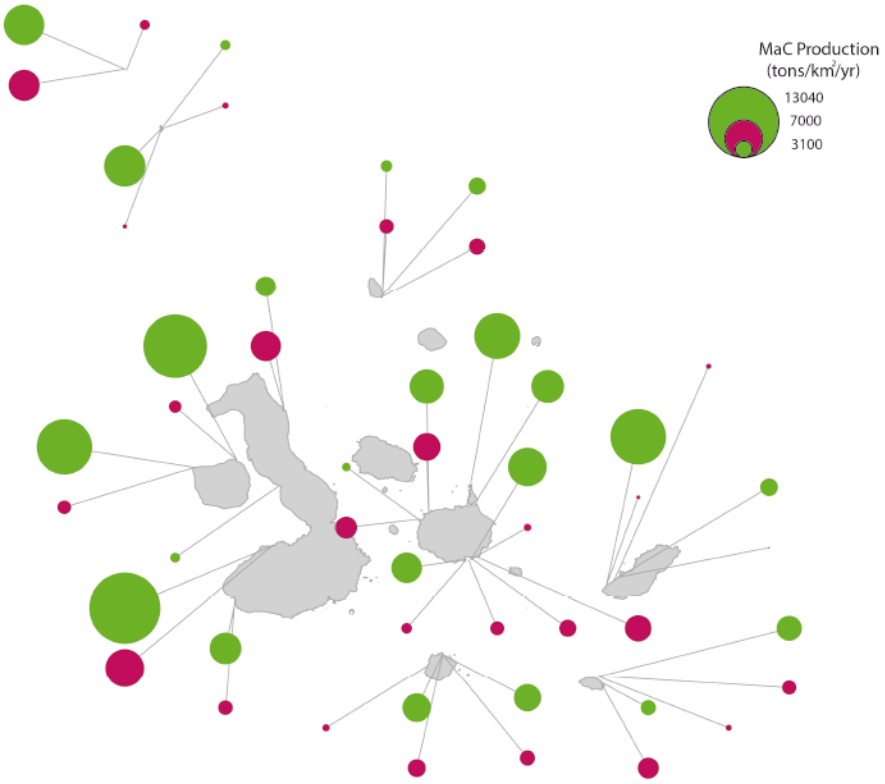

Figure 4: MaC production per transect, circle sizes are relative to production values in tons/km^2/yr. Where circles are stacked vertically, transects were performed at both depths, with 6m production values (in green) above 15m production values (in red).

Production was greater in 6m (5923.69 +/-3239.06) than in 15m (2606.97 +/-1709.12); t = 4.3505, df = 30.074, p-value = 0.000144 (Figure 5).

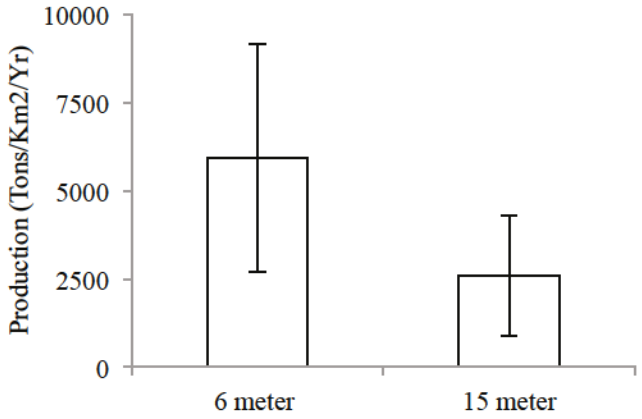

Figure 5: Average estimated MaC production per depth (6 m n = 22, 15 m n= 28). Error bars represent standard deviations.

Biomass and Production Relationship:

Biomass and production per transect were positively correlated (p-value = 0.002199, Figure 6), though with high variability ($R^2 = 0.17909$).

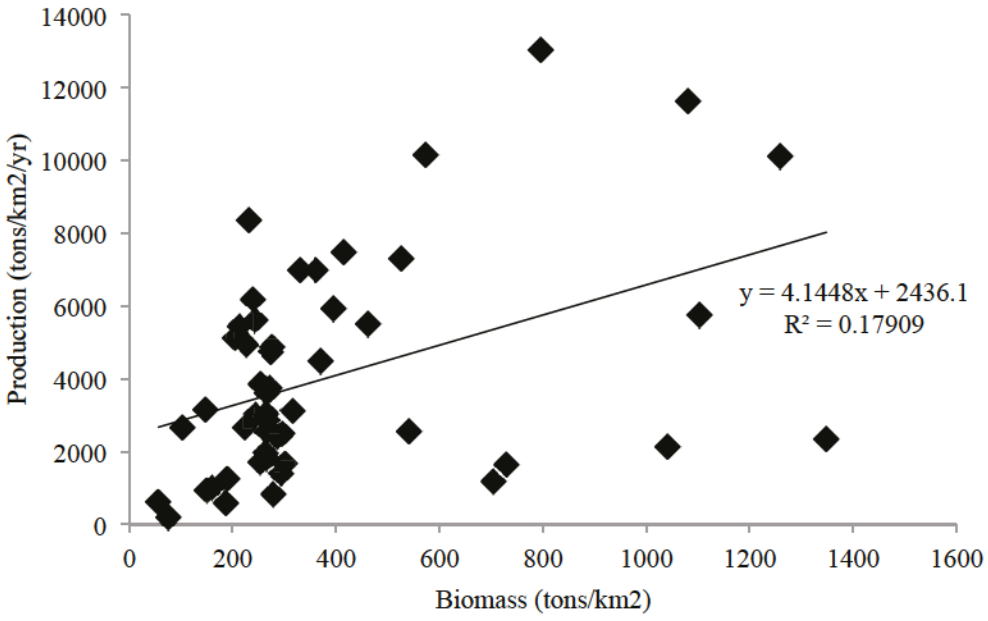

Figure 6: Relationship between macroalgal Production and Biomass.

Production per Biomass (P/B):

Calculated P/B for each functional group ranged from 0.629 for 'Calcareous Crustose' to 109.30 for 'Microalge' (Table 2).

Table 2: Calculated parameter values per functional group. SF_{fg} = Scaling Factors, P_{fg} = Production (tons/km^2/yr).

Functional Group	SF_{fg}	P_{fg}	B_{fg}	P/B_{fg}
Microalgae	1.97044335	27949.37931	255.71	109.30
Filamentous	1	14184.310	306.52	46.28
Thin Foliose	1.25862069	17852.66603	1079.17	16.54
Thick Foliose	0.1908867	2707.596121	2650	1.0217
Corticated Branching/Bushy	0.294334975	4174.938534	2101	1.987
Leathery	0.201970443	2864.811379	4240	0.676
Articulated Calcareous	0.077586207	1100.50681	833.33	1.321
Crustose Calcareous	0.011083744	157.2152586	250	0.629
Non-Calcareous Crustose	0.049261084	698.7344828	307.69	2.271

MaC P/B per transect ranged from 1.65 in 15m at La Botellita (Floreana, FL04) to 35.96 at Canal Itabaca (Santa Cruz, SC09; Figure 7). P/B averaged 14.48 +/- 7.55 in 6m and 10.54 +/- 7.71 in 15m ($t = 1.8154$, $df = 45.667$, p-value = 0.07603).

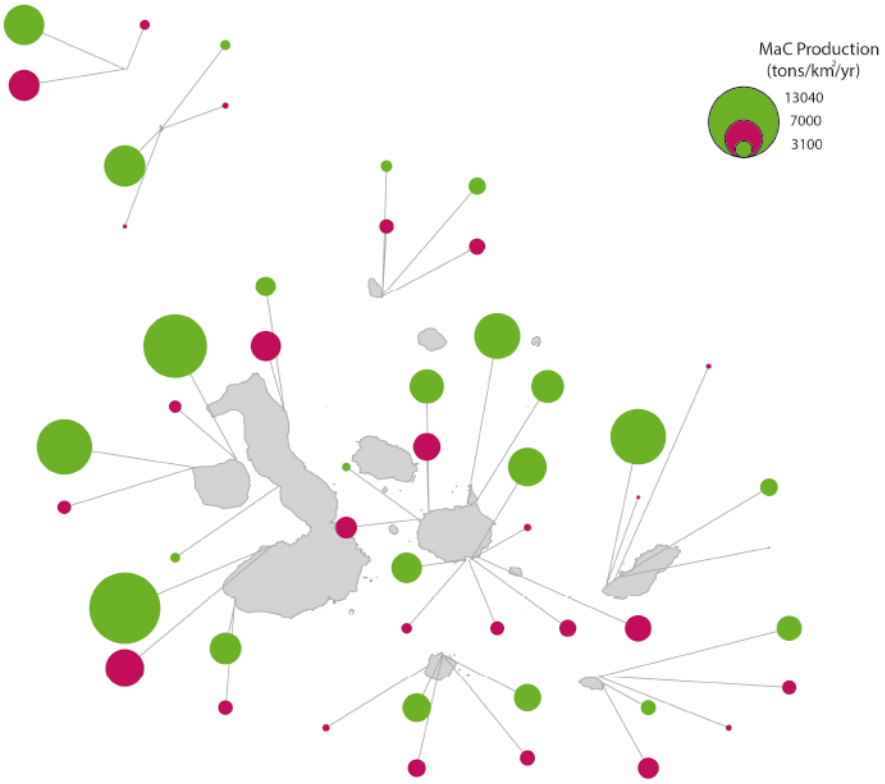

Figure 7: MaC Production/Biom ass (P/B) per site, circle sizes are relative to (P/B) values in tons/km2/yr. Where circles are stacked vertically, transects were performed at both depths, with 6m production values (in green) above 15m production values (in red).

In situ study at two depth strata:

Overall total MaC production (tons/km^2/yr) was found to be greater (t = 7.7259, df = 34.701, p-value = < 0.0001) in 6m cages (10792.70 +/-2587.12; n = 22) than in 15m cages (5504.41 +/- 1687.10; n = 19). Growth was dominated by foliose and filamentous groups. Differences between these production values and those estimated by surveys (site SC12 in Chapter 2, 6m P = 6983.12, 15m P = 1240.293) was 3809.58, (35.2% of transect P) in 6m, and 4264.117 (77% of transect P) in 15m. In theory, these differences can be attributed to the consumption by macroherbivores that were excluded by the cages. Control scrapings (n = 20 per depth) did not change significantly (no net growth outside cages) over the sampling period.

Functional Group Influence:

Cover of the 'Filamentous' group had the most positive influence on P/B per transect, and cover of 'Thick foliose' had the most negative influence (Figure 8, Table 3).

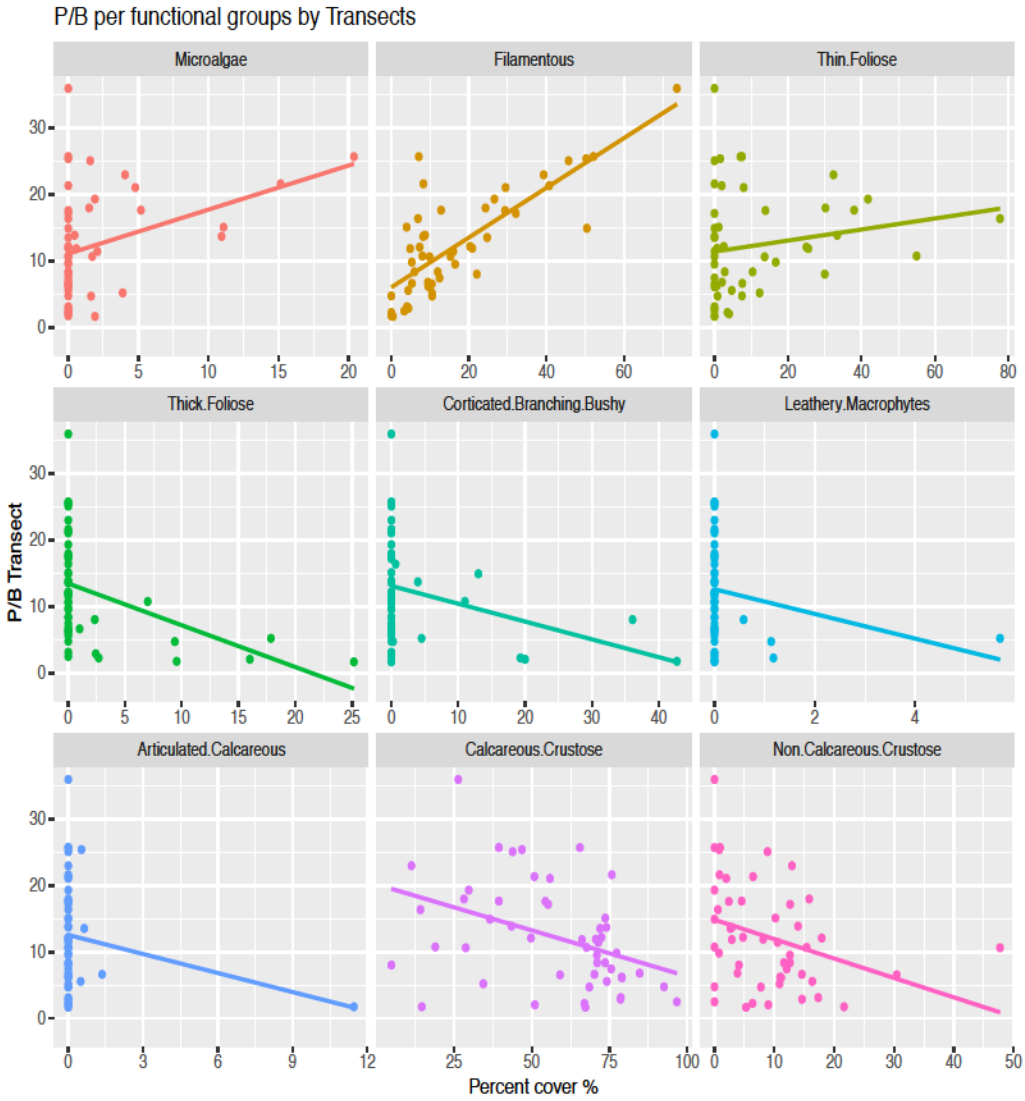

Figure 8: Regressions of P/B vs. % cover of functional groups per transect.

Table 3: P/B vs. % cover of functional groups regression statistics per transect.

Functional group	R^2	R adjusted	P value
Microalgae	0.1227	0.1044	0.01266
Filamentous	0.6168	0.6088	1.45E-11
Thin Foliose	0.03089	0.0107	0.2221
Thick Foliose	0.1692	0.1519	0.003003
Corticated Branching/Bushy	0.09054	0.07159	0.03372
Leathery	0.03926	0.01924	0.1678
Articulated Calcareous	0.0396	0.01959	0.1659
Crustose Calcareous	0.1611	0.1436	0.003869
Non-Calcareous Crustose	0.1089	0.0903	0.01928

Regional Biomass, Production, and P/B:

Biomass in the Western region was more than three times higher (ANOVA p-value = < 0.0001) than in the North or Central/South, which did not vary from each other (Figure 1A, Table 3). Production was also higher (ANOVA p-value = 0.050) in the West than the Central/South (post hoc p-value = 0.0436), but did not vary between Western and North regions (post hoc p-value = 0.1736), or between North and Central/South (post hoc p-value = 0.0431). Production/Biomass ratios did not vary significantly (ANOVA p-value = 0.15) across regions.

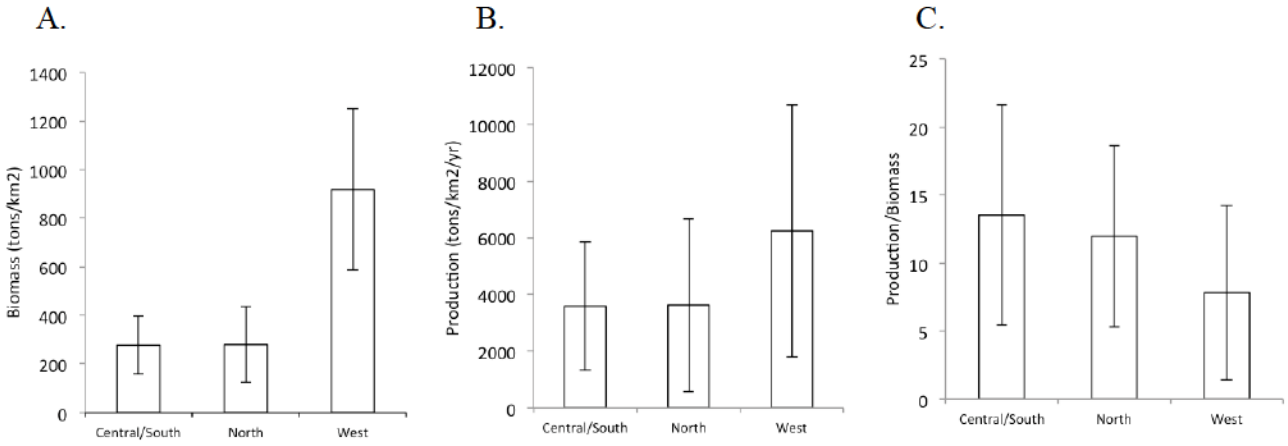

Figure 9: Regional means of macroalgal (A) Biomass, (B) Production, and (C) Production/Biomass. Error bars represent standard deviations.

Table 4: Regional means of Biomass (B; tons/km^2), Production (P; tons/km^2/yr), and Production/Biomass (P/B). SD = standard deviations

Region	B	SD	P	SD	P/B	SD
Central/South	277.562	120.012	3582.627312	2263.141944	13.51436326	8.093853932
North	279.922391	156.1373293	3620.416553	3052.983046	11.97549946	6.645185416
West	918.8002175	331.5461371	6240.447522	4442.509143	7.818477517	6.438912271

ENSO Index:

The MEI range over the sampling period (Jun 2012-Sep 2014) indicates weak "El Niño" in 2012 transitioning to weak "La Niña" conditions in 2013 and 2014 (Figure 10).

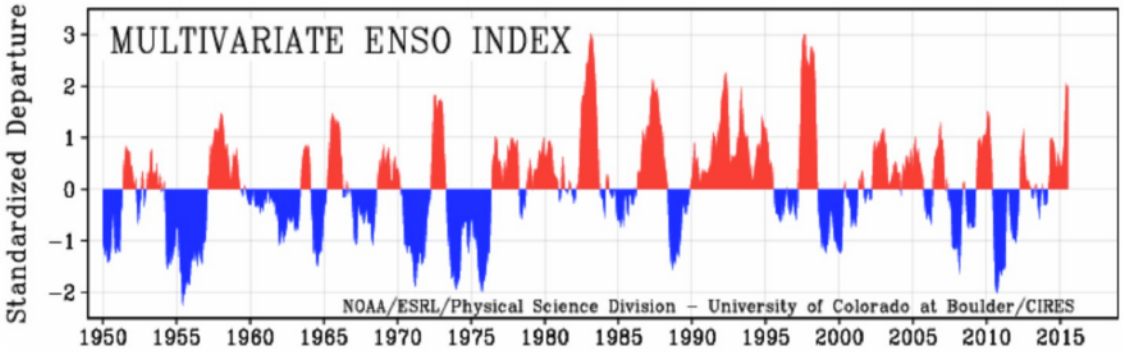

Figure 10. Long-term variation in the MEI.

The mean MEI rank score (https://www.esrl.noaa.gov/psd/enso/mei/rank.html) over the sampling period was 35.98. Using 30th percentile rankings, MEI ranks from 1-20 denote strong to weak La Nina conditions, while 48-67 denote weak to strong El Nino conditions. Therefore the sampling period can be described as "ENSO-Neutral."

DISCUSSION

Our results show that geographic variation in MaC parameters are likely responsible for the differences reported in previous trophic models. In addition, overall cover of MaC, community composition, and depth-related variation in production are important factors to account for during model parameterization. Given the ENSO-neutral oceanographic conditions during sampling, these results can be used as baselines to quantify changes in MaC parameters during ESNO events.

Regional differences in biomass and production values are likely the result of both environmental and biological influences, which create gradients of stress or disturbance in the system. The 'Western' region is considered to be the most oceanographically stable and productive, due to the upwelling influence of both the EUC and the Humboldt Current. The macroalgal community in the West was generally more functionally diverse,

and composed of greater overall cover of groups with high biomass, though with lower overall productivity (e.g. 'Corticated Branching/Bushy' and 'Leathery' groups). These groups are composed of generally more perennial, or longer-lived species. Presence of these groups is therefore indicative of a more mature MaC, with more stability and less species turnover. The 'Central/South' and 'North' regions were generally much lower in overall MaC biomass, but had high cover of very productive groups ('Microalgae,' 'Filamentous,' and 'Thin Foliose') leading to disproportionately higher P/B ratios. These highly productive groups are generally more opportunistic and ephemeral, indicating a higher level of disturbance or instability in the 'Central/South' and 'North.'

Variation in cover of MaC across transects is very important for determining biomass and production. For example, some transects with community composition dominated by the most productive functional groups (e.g. 'Filamentous,' 'Thin Foliose') were calculated to have relatively low overall production, due to low overall cover of MaC (high cover of sand or sessile invertebrates). For example, the MaC of both the 15m transect at Las Cuevas (Floreana, FL06, 30.21%) and the 15m transect at Punta Cormoran (Floreana, FL13, 50.38) was composed of high cover (52.11 and 40.69%, respectively) of the productive 'Filamentous' group. However, low overall cover of MaC (30.21 and 50.38%, respectively), lead to overall low production values for these transects. Therefore variation in the overall cover of MaC is necessary to account for when calculating parameters.

Due the variable relationships between P/B across functional groups, MaC community composition (independent of overall biomass) is very important for determining MaC production. An extreme example would be the difference in production values between the 6m transect at Las Cuevas (Floreana, FL06) and the 15m transect at Isla Lobos (San Cristobal, SB06). Estimated biomass (tons/km^2) per transect was relatively similar (277.53 and 280.34, respectively), while estimated production (tons/km^2/yr) varied six-fold (4884.00 and 805.69, respectively), as did P/B ratios (17.60 and 2.87, respectively).

At Las Cuevas, MaC biomass consisted primarily of 'Crustose Calcareous' (49.20 % of total), and 'Thin Foliose" (23.01 %). At Isla Lobos MaC biomass consisted primarily of 'Crustose Calcareous' (61.53 % of total), and 'Thick Foliose" (20.10 %). The variation in MaC production between these sites was therefore due primarily to the large difference in P/B between the 'Thin Foliose' and 'Thick Foliose' groups.

Understanding variability in MaC across depths is important to our knowledge of the system. Globally, macroalgae thrive in intertidal systems, but have also been found living at over 250m in depth (Litter et al., 1985). Across this depth range, great variations in MaC composition have been reported. This work, therefore, presents only a limited understanding of the influence of depth on MaC parameters in the Galapagos. Reports and observations of abundant MaC in intertidal habitats in Galapagos are common, and several authors have described abundant MaC (including forests of the kelp *Eisenia*

galapagensis) in deeper (>20m) waters (Tompkins & Wolff, 2017). Beyond the information presented here, to date little information exists regarding variability in MaC community characteristics across the full depth range of potential growth in the Galapagos.

However, the difference in MaC biomass and production parameters between the two depths surveyed presents a real and interesting pattern. In many instances, urchins were more abundant in deeper transects compared to shallow, and the reverse pattern was noted for damselfish. High densities of urchins are known to inhibit MaC diversity and overall growth, and can ultimately create 'barrens' covered by 'Calcareous Crustose' algae, or even bare rock (Steneck, 2013). Meanwhile, damselfish actively "farm" filamentous forms of algae while defending their territories from all competitors (Irving & Witman, 2009). In the Galapagos, these competitors include urchins and large schools of surgeonfish, parrotfish, and chubs, which may graze preferentially in deeper water to avoid harassment by damselfish.

In situ results (Caamaño, herbivore cages) suggest that grazing by macroherbivores (herbivorous fish and large urchins) is important for determining overall MaC biomass, and can perhaps account for the majority of consumption in the system. However, these grazers were not an important factor in depth-related differences in actual MaC production. Other factors, such as local water transparency and light levels, sand scour, and meso-grazers could be influencing this difference, and should be accounted for.

Meso-grazers and microphytobenthos could represent a "lost trophic groups" in the system. Meso-grazers such as arthropods (amphipods), echinoderms (urchin recruits), mollusks (snails, limpets), even fish (recruits or small juveniles of herbivorous species) etc. can be abundant in macroalgal habitats, and are usually not accounted for in functional group classification (Brawley, 1992). This is also true of microbial sources of primary productivity, such as benthic unicellular diatoms or bacteria, which form productive biofilms on a variety of substrates (Macintyre et al 1996). Though visible filaments and mats of microbes were recorded here as part of the MaC in Galapagos, these methods may be overlooking other potentially important benthic components of the trophic web.

Overall, this work offers a methodological framework and quantitative baseline for studying future changes in macroalgal ecological parameters in the Galapagos. In the past, strong El Niño's have been associated with crashes in populations of macroalgal grazers in the Galapagos (e.g. marine iguanas), indicating declines in MaC production. Shifts in composition of MaC during ENSO events have also been described in the archipelago, but were never before directly measured at a large scale (Kendrick, 1988). Understanding how both regional and temporal variation in these parameters affects the MaC production available to higher trophic levels will greatly improve the accuracy of ecosystem-level predictions of energy flow structure in the Galapagos marine food web.

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Chapter 4: Origins and ecological significance of *Caulerpa* in the Galapagos Marine Reserve

Abstract: Over the last century however, environmental changes combined with exponentially increasing human activities in the Galapagos archipelago (Ecuador) have raised concerns about the introduction and colonization of invasive marine species. *Caulerpa*, a macroalgal genus implicated in invading and degrading marine ecosystems, has been recently observed as abundant and overgrowing corals in 10-15 m depth on a coral reef near Darwin's Arch on Darwin Island. This work is part of a Charles Darwin Foundation (CDF, Darwin Initiative) and Galapagos Conservancy funded project aiming to predict and minimize the negative impacts of marine invasive species like *Caulerpa* on the overall ecological health of the Galapagos Marine Reserve. Here we present information on the history/potential origins, systematics, and ecological behavior of *Caulerpa*. *Caulerpa* was first registered in the Galápagos Islands in 1899, and has been reported consistently since. Early reports were restricted to intertidal habitats, where it was reported in abundance at one location in 1936. Historical collections, descriptions, and reports of *Caulerpa* have been generally limited to the previously named *C. racemosa* and/or *C. peltata*, or variations of these two growth forms. *tuf*A sequences obtained from six specimens (from Tortuga Bay and Academy Bay on Santa Cruz Island, and Puerto Villamil on Isabela Island) corresponde to *C. chemnitzia* and *C. racemosa,* two entities previously identified in the Eastern Pacific (Fernández et al. 2016), which are are also found pantropically (Sauvage et al. 2012) and belong to the polyphyletic complex of raceme/shield-forming *Caulerpa* species. Cover of *Caulerpa* was not recorded in 2012 at Darwin's Arch, but by 2014 had reached 15%, exceeding that of live coral. We discuss future initiatives for monitoring *Caulerpa's* behavior in the GMR, including futher surveys and genetic barcoding, and stress vigilance across stakeholder groups in order to identify any potential future invasions.

Keywords: Galapagos, invasive species, *Caulerpa*, ecological monitoring, phylogenetics

INTRODUCTION

Species of the infamous green algal genus *Caulerpa* are known as widespread and tenacious marine invaders, among which *Caulerpa taxifolia* is listed as one of the 100 most invasive species in the world (Lowe et al., 2000; Schaffelke et al., 2006). After being introduced in the Mediterranean Sea in the early 1990's, *C. taxifolia* blanketed shallow benthos, defying all eradication efforts while smothering native competitors. This caused drastic biodiversity declines in an already-stressed ecosystem (Meinesz et al., 2001). Although less publicized, *C. cylindraceae* (previously known as *C. racemosa* or *C. racemosa* var. *cylindraceae*) was also introduced into the Mediterranean, and in less than two decades rapidly spread to 11 different countries and all major islands of the basin via opportunistic and aggressive colonization of varied benthic habitats (Klein & Verlaque, 2008). Even in their native ranges, *Caulerpa* species have been reported to grow rapidly, particularly in disturbed areas where they can overgrow and out-compete other macrophytes and reduce local biodiversity (Zhang et al., 2014). While efforts to eradicate *Caulerpa* have met with some success, these usually involved costly and destructive methods that cannot discriminate introduced from native taxa (e.g. tarping and chlorine treatment of *C. taxifolia* in Southern California; Anderson, 2005).

Globally, coral reefs are being lost at an ever-increasing rate, often as a result of algal overgrowth (Pandolfi et al., 2005). This overgrowth is facilitated by loss of important algal grazers (overfishing), increasing nutrient inputs (eutrophication), climate-change induced warming of surface waters, and ocean acidification (McCook et al., 2001, Littler et al., 2006, Hughes et al., 2007, Diaz-Pulido et al., 2011). Whether native or introduced, invasions by *Caulerpa* species have been reported in temperate and tropical latitudes worldwide, and generally negatively affect corals. Such invasions have been documented from several locations worldwide, such as the Arabian Gulf (Vanneyre et al. 2014), Panama (Glynn & Mate, 1997, Smith et al. 2010), the Adriatic (Kružić et al., 2008), Florida (LaPointe & Bedford, 2010), Maldives (Montano et al., 2012), Gulf of California (Perez-Estrada et al., 2013), and Costa Rica (Fernandez & Cortez, 2005). Implicated in ecosystem degradation and overall marine biodiversity declines, invasive *Caulerpa* species are the focus of exhaustive investigations into their introductions, history/potential origins, systematics, and ecological roles (e.g. Durand et al., 2002; Verlaque et al., 2003; Smith et al., 2010).

Over the last century, several *Caulerpa* species have been reported in the Galapagos Islands (Table 1), a volcanic archipelago 1,000 km off the coast of Ecuador in the Tropical Eastern Pacific. Due to its geographic isolation and location at the confluence of several major Eastern Pacific Ocean current systems, the Galapagos hosts diverse and unique biological communities. These are found within UNESCO World

Heritage Sites (UNESCO 2016) of the Galapagos National Park (GNP) and the Galapagos Marine Reserve (GMR). The GMR remains one of the most unique, productive, and well-conserved tropical marine ecosystems on earth. Over the last century however, environmental changes combined with exponentially increasing human activities in the GMR (e.g. fishing, mainland cargo shipping, inter-island marine traffic) have raised concerns about the introduction and colonization of invasive marine species (Keith et al., 2016).

Moreover, recent combined effects of strong ENSO events, increased urchin abundances and overfishing in the Galapagos, (Edgar et al., 2010) have disturbed marine ecosystems, providing opportunities for fast-growing benthic species to proliferate and cause local extinctions. For instance, following the strong 1982/'83 ENSO event, a mortality rate of up to 95-99% was estimated for corals archipelago-wide (Glynn, 1988), and the once common and dominant species of fucoid algae *Bifurcaria galapagensis* seemingly went extinct (Kendrick, 1988; Tompkins, 2017). Since 1983 urchin abundances and the formation of barrens also seemingly increased in the GMR (Edgar et al, 2010), a phenomenon previously linked to overfishing of urchin predators in the archipelago (Sonnehozer et al., 2009). While urchins in general can limit macroalgal and sessile invertebrate recruitment and growth, urchin grazing has limited effect on already established *Caulerpa* species (Cebrian et al., 2011) and disease outbreaks in over-abundant urchin populations can decimate populations occupying barrens, suddenly leaving them empty (Leinaas & Christie, 1996) and consequently opening space for fast-growing, opportunistic, and competitively dominant benthic species.

Since 2012, Charles Darwin Foundation (CDF) researchers have been working on a Darwin Initiative and Galapagos Conservancy funded project aiming to predict and minimize the negative impacts of marine invasive species on marine biodiversity, ecosystem services, and the overall health of the GMR (Keith 2016). Due to its generally invasive nature and recent reports of locally increasing abundance, *Caulerpa* is now a focal species of this project, and has been included in the CDF's 'Watch List' of species to monitor. Taxonomically, *Caulerpa* species are notoriously challenging because of the large amount of intraspecific plasticity and morphological convergence that some species may exhibit, and generally require DNA sequencing (i.e. barcoding) to aid/confirm their identification.

As such, this work seeks to inform the CDF's *Caulerpa* research by presenting historical reports and collections, resolving their most current taxonomy relying on tufA barcoding, and providing baseline cover of *Caulerpa* on the iconic coral reef of Darwin Island in the GMR. In the discussion, this information is synthesized and applied to the pool of Galapagos marine ecosystem knowledge in order to forecast potential future ecological impacts of *Caulerpa* species in the shallow marine ecosystems of the GMR. In particular, we discuss current and future interactions between *Caulerpa* and corals, and the influence of predicted changes in ocean temperature and chemistry on this

relationship. Finally, monitoring and management recommendations are presented for *Caulerpa* species in the GMR.

METHODS

Historical reports and collections:

Relevant publications, grey literature, and the CDF database were accessed and reviewed to extract the historical record and associated collection information (year, location, habitat, collector, species) of *Caulerpa* species in the Galapagos, particularly the earliest reports from islands or regions, or repeated reports after long (>10yr) lapses in time. For example, replicate collections or reports from identical or nearby sites made over short time periods were considered as redundant and not included here. Herbarium collections (CDF, University of California Berkeley, University of Michigan, University of North Carolina Wilmington) for the genus were also accessed and relevant information from significant collections extracted.

Taxonomy and preliminary phylogenetics:

Caulerpa taxonomy and phylogeny is an ongoing venture in phycology. The most recent publications regarding taxonomy of the species and/or forms of *Caulerpa* reported and/or collected in Galapagos to date were referenced for this work. During 2012-2013, *Caulerpa* samples were collected throughout the archipelago, photographed, described, pressed, and added to the CDF Herbarium collection and Database. Representative sub-samples were dried in silica and extracted and sequenced for the gene *tuf*A in the Seaweeds Laboratory at the University of Louisiana at Lafayette. These were compared with other available *Caulerpa* sequences on GenBank to determine their molecular identity and most appropriate species name based on currently accepted taxonomy. Selected *tuf*A sequences were clustered with newly generated data in MEGA v7 (Kumar et al. 2016) and the tree edited in FigTree, clades collapsed for simplicity (A. Rambault, tree.bio.ed.ac.uk).

Baseline cover on a coral reef:

Cover of *Caulerpa* species at Darwin Island in the far north of the archipelago was quantified along 50 m transects placed parallel to shore at 15 m depth at two iconic and popular dive-tourism and CDF monitoring sites: Arco Darwin (1.673480N, 91.991385W) and Arricife Antiguo (1.674647N, 91.992228W). Along each transect, 10 replicate 80 cm^2 quadrats spaced 5 m apart were digitally photographed at a standardized perpendicular distance of 0.75 m from the substrate. Digital images were then analysed using Vidana 1.0.1 (tracing polygons of highest substrate level) to quantify percent cover per quadrat of the main benthic/functional groups including '*Caulerpa*', 'Coral',

'Crustose Coralline Algae' (abbreviated CCA hereafter) and 'Other Algae'. Averages ±SD per group were then plotted for each site. These methods were designed for rapid, low cost, and repeatable ecological data acquisition to facilitate future monitoring. Such methods and data can be readily incorporated into the CDF's pre-existing ecological monitoring program.

RESULTS

Historical reports and collections:

Caulerpa was first registered in the Galápagos Islands in 1899 on the Island of Isabela by Farlow (1902) as *C. racemosa* var. *clavifera* (Table 1). Since then, additional records were made from five more of the archipelago's islands under the same subspecific epithets, or other varieties of *C. racemosa*, as var. *occidentalis* or var. *uvifera* (e.g. Setchell & Gardner 1937; Taylor 1945) (Table 1; Figure 1). Several specimens were also reported as *Caulerpa peltata* (e.g. Taylor 1945, and in UCB and FCD collection, see Table 1). A single record was made for *Caulerpa ambigua* Okamura as *C. vickersiae* Børgesen by Dawson (1963), a previously used epithet for this very diminutive taxon (Draisma et al. 2014), which has not been reported since but could have been easily overlooked. Prior to 2012 the only mention of *Caulerpa* in abundance was in 1936 by Taylor (1945, as *C. racemosa*), who noted "immense beds" covering the bottom of an inland salt-water lagoon on Fernandina Island (exact location unknown, Table 1, see footnote). The remainder of historical reports are of sparse patches. In 2012, *Caulerpa* (then as *C. racemosa*) was reported as abundant in a protected lagoon near Tortuga Bay (Playa Mansa) on Santa Cruz Island, and as increasing in abundance near Puerto Villamil on Isabela Island (D. Acuña and J Suarez, pers. comm). In 2013, *Caulerpa* (then as *C. peltata*) was observed as abundant and overgrowing corals in 10-15 m depth on a coral reef near Darwin's Arch on Darwin Island (D. Acuña pers. comm, and pers. obs.).

Table 1. Reports of *Caulerpa* in the Galapagos, in chronological order.

Year	Island	Locality	Habitat	Collector/ID	Recorded As*	Reference
1899	Isabela	Tagus Cove	Intertidal	R.E. Snodgrass, E. Heller/Farlow	*C. racemosa var. clavifera*	Farlow, 1902
1932	Fernandina	S.E. Coast	Intertidal	J.T. Howell	*C. racemosa var. clavifera*	Setchell & Gardner, 1937
1932	Fernandina	N.E. Coast	Intertidal	J.T. Howell	*C. racemosa var. occidentalis*	Setchell & Gardner, 1937
1932	Isabela	Puerto Villamil	Intertidal	J.T. Howell	*C. racemosa var. clavifera*	Setchell & Gardner, 1937
1932	Santa Cruz	Academy Bay	Intertidal	J.T. Howell	*C. racemosa var. clavifera*	Setchell & Gardner, 1937
1934	Wolf	Anchorage	Intertidal, abundant in lower pools	W.R. Taylor	*C. peltata*	Taylor, 1945
1934	Española	Gardner Islet	Intertidal	W.R. Taylor	*C. peltata*	Taylor, 1945
1934	Floreana	Black Beach Anchorage	Intertidal	W.R. Taylor	*C. racemosa var. uvifera*	Taylor, 1945
1934	Fernandina	Undetermined	Bottom of salt-water lagoon, 1.5 m depth**	W.R. Taylor	*C. racemosa var. occidentalis*	Taylor, 1945
1962	Santa Cruz	Tortuga Bay	East inner lagoon, intertidal	E.Y. and C.M. Dawson	*C. racemosa var. occidentalis*	UCB Collections
1962	Santa Cruz	Tortuga Bay	East inner lagoon	E.Y. and C.M. Dawson	*C. vickersiae****	Dawson, 1963

1962	Santa Cruz	Punta Nuñez	Intertidal	E.Y. and C.M. Dawson	*C. racemosa var. clavifera*	UCB Collections
1962	Santa Cruz	Academy Bay	Intertidal	E.Y. and C.M. Dawson	*C. peltata*	UCB Collections
1974	Floreana	Champion Islet	Subtidal, -4m, on coral	G.M. Wellington	*C. peltata*	FCD Collections
2002	Darwin	El Arco	Subtidal, -9m, on coarse sand, site of high exposure	L.E. Garske	*C. racemosa*	FCD Collections
2012	Isabela	Puerto Villamil	Intertidal	D. Acuña (FCD)	*C. racemosa*	FCD Collections
2012	Santa Cruz	Tortuga Bay	East inner lagoon, intertidal and shallow (-1m) subtidal	J. Suarez (FCD)	*C. racemosa*	FCD Collections
2012	Santa Cruz	Academy Bay, BIOMAR Reef	Intertidal	P. Tompkins	*C. racemosa, C. peltata*	FCD Collections
2013	Darwin	El Arco and Arricife Antiguo	Subtidal, 10-15 m depth, overgrowing dead and live coral	D. Acuña/P. Tompkins	*C. peltata*	FCD Collections

*With the exception of *C. vickersiae*, all reports listed here are tentatively considered to be of *C. racemosa or chemnitzia* (Belton et al. 2014), until further genetic results are made available.

**The bottom of an inland salt-water lagoon (several such lagoons exist on Fernandina) was reported to be "covered with immense beds of *Caulerpa racemosa*. (Taylor 1945)."

***Currently accepted as *C. ambigua,* Draisma et al. 2014.

NOTE: W.R. Taylor collected *C. racemosa var. peltata* and *C. peltata* on the mainland in 1933 and 1934, at La Libertad and Santa Elena Point (Santa Elena, Ecuador), respectively (Taylor 1945). M. Ragan collected *C. sertularioides f. longpipes* and *C. sertularioides f. longiseta* on the coast of Ecuador in Playas (Guayas) in 1974 (UNC Wilmington Herbarium collection) but has not been recorded in the Galapagos. The species did exist on the mainland in areas near marine traffic routes to Galapagos.

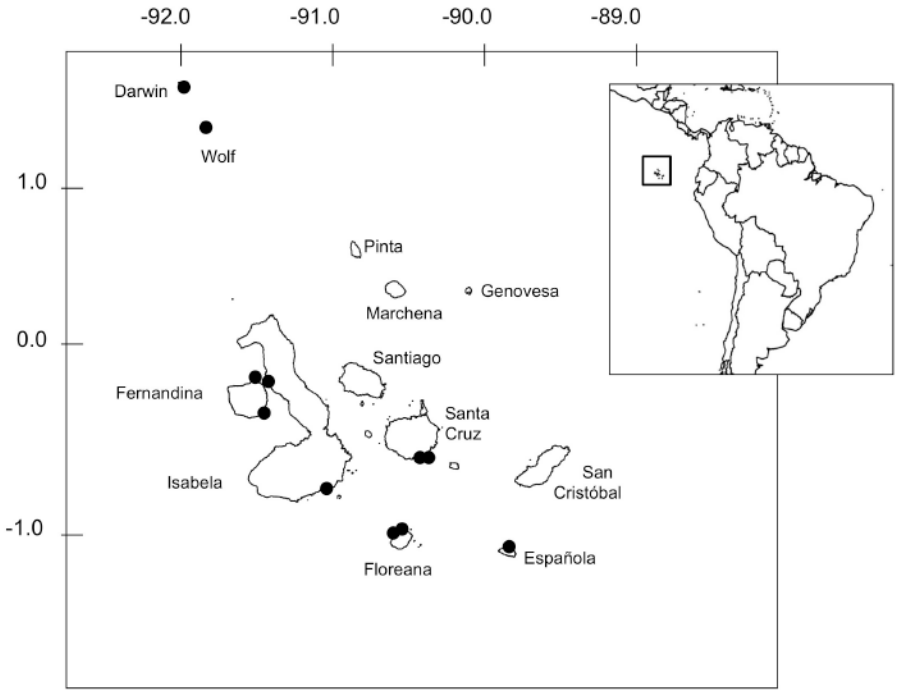

Figure 1. Locations of historical reports and collections of *Caulerpa* in the GMR. Base map courtesy of D. Ruiz.

Taxonomy and preliminary phylogenetics:

Historical collections, descriptions, and reports of *Caulerpa* have been limited to the previously named *C. racemosa* and/or *C. peltata*, or variations of these two growth forms. General thallus structure is of stalked, 1.5-3mm diameter ramuli emerging radially in 3-6 ranks from 2-7 cm length assimilators which arise from a branching, 1.5-3 mm diameter stolon anchored to the substrate by rhizoids. This habit fits the historically named *C. racemosa-peltata* complex, or variations of that name. This was the most "taxonomically troublesome" group in the *Caulerpa* genus, until recent genetic analysis identified members of this complex as monospecific: *C. chemnitzia* (Belton et al. 2014).

Like other macroalgal species, *Caulerpa* exhibits intraspecific phenotypic plasticity across environmental gradients (e.g. Svedelius, 1906; Collado-Vides 2002), and variation in ramuli shape and lengths of pedicels and assimilators of *C. chemnitzia* in Galapagos may be a response to factors such as hydraulic energy and/or depth. Ramuli shape varies from near-spherical or globular to strongly peltate with indented margins (supplemental images), and assimilator lengths range from 2-7 cm, with intra-individual assimilators often being of similar lengths. *C. chemnitzia* was reported and collected

across a range of wave exposures and depths, and morphologies followed a general pattern: Long assimilators (4-7 cm), and large, globular (spherical), and sparse ramuli of thalli occurring in shallow protected lagoons on Santa Cruz (J. Suarez and D. Acuña collections) and Fernandina Island (Taylor, 1945 collection); and shorter assimilators (2-3 cm) with dense and peltate ramuli occurring on low-intertidal wave-swept benches in Academy Bay (P. Tompkins, collection and pers. obs.), and to 15 m depth on a high-current coral reef (Darwin Island, D. Acuña collection and P. Tompkins pers. obs.).

*tuf*A sequences obtained from six specimens (from Tortuga Bay and Academy Bay on Santa Cruz Island, and Puerto Villamil on Isabela Island) corresponded to two entities (species clade) previously identified in the Eastern Pacific (Fernández et al. 2016), which are are also found pantropically (Sauvage et al. 2012; Figure 2). These belong to the polyphyletic complex of raceme/shield-forming *Caulerpa* species (previously termed the *C. racemosa-peltata* complex), whose multiple clades were recently reinstated according to basionyms (Belton et al. 2013). According to this currently accepted taxonomy of the complex, the two clades present in the Galapagos correspond to *C. chemnitzia* and *C. racemosa* (pantropical lineages A and D respectively, *sensu* Sauvage et al. 2013). The invasive Mediterranean alien *C. cylindraceae* (Belton et al. 2013) native to Australasia (previously as *C. racemosa* var. *cylindraceae*, see Lineage F *sensu* Sauvage et al. 2013), is genetically very distant from the Galapagos samples sequenced to date and thus unlikely present locally.

Morphologically, lineages A and D differ slightly in the shapes of bladelets and lengths of pedicels, but greater phenotypic plasticity in lineage A can easily cause morphological overlap. More importantly, the known invasive and Mediterranean alien Lineage F (var. *cylindracea*) is native to Australasia, and is genetically very different from the Galapagos samples sequenced to date. This lineage was also introduced to Adelaide in 2001 where it continues to compete for space and cause ecological changes in the environment (Collings et al. 2004).

Figure 2: tufA sequencing-based phyloegenetic tree including all Galapagos *Caulerpa* samples sequenced to date. Species clades of the previously named '*C.racemosa -peltata*' complex are listed in bold, and newly sequenced specimens are marked with an asterisk. Introduced and invasive taxa elsewhere are marked with a warning symbol, and shown to be widely divergent with taxa found in the Galapagos, namely *C. chemnitzia* and *C. racemosa*. Bootstrap values below 50 not shown.

Baseline cover on a coral reef:

The survey method proved to be rapid, 10-15 minutes per transect, and results obtainable within an hour of data collection. *Caulerpa* and corals showed similar coverage (20.33 +/- 11.55 % and 23.11 +/- 18.67 %, respectively) at Arricife Antiguo (Figure 2) while the abundance of *Caulerpa* (15 +/-15.08 %) exceeded that of coral (5.38 +/- 12.43 %) at Darwin's Arch, a popular dive site. CCA were more abundant at Arrecife Antiguo. At both sites, *Caulerpa* was commonly seen overgrowing *Pocillopora* (supplemental images). Caulerpa by itself represented a large amount of the algal cover compared the other fleshy algal species combined (see 'Other algae' group, Figure 3).

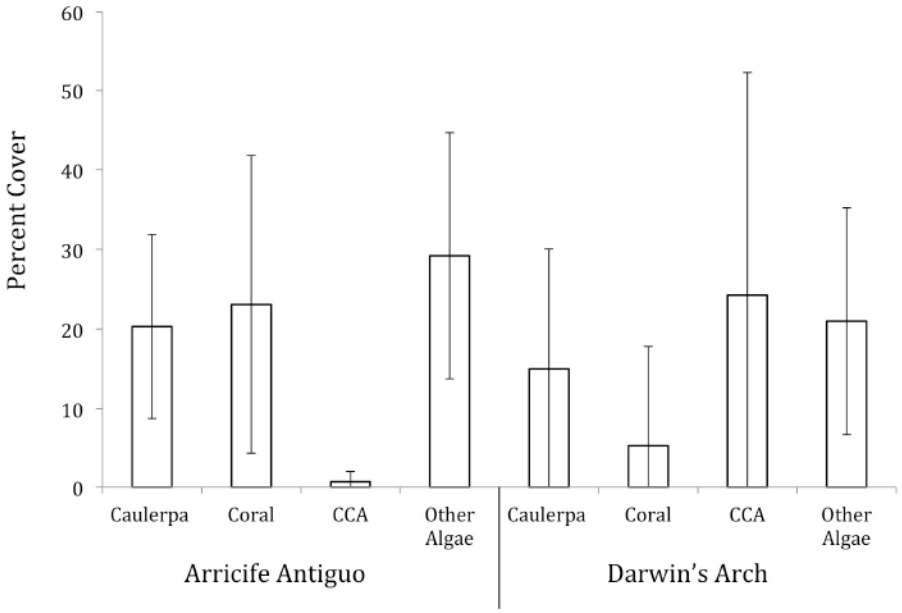

Figure 3. Percent cover of main benthic groups at 15 m depth at Arricife Antiguo and Darwin's Arch, Darwin Island, Galapagos.

DISCUSSION

Origins and identification:

Since the discovery of Galapagos in 1535, the archipelago was used as a base of operations for English pirates in the late 1600's, whalers in the late 1700's, and privateers during the war of 1812 (Galapagos Conservancy, 2016). The first permanent colony was established in 1869, and since then Galapagos has been subjected to ever-increasing marine traffic. Fouling of untreated ship hulls is a common vector for alien macroalgal species introductions (Hewitt et al., 2007; Mineur et al., 2007), and while "natural" colonization of the Galapagos by *Caulerpa* is plausible and likely, it is also possible that *Caulerpa* was first introduced to the islands in the 17th or 18th centuries on wooden ship hulls, potentially repeatedly. Given available space for settlement and growth, the alternative dispersal mechanisms in *Caulerpa* species (via vegetative fragments, zygotes, and propagules) and the dynamic surface current regimes in Galapagos would have allowed for its rapid and widespread colonization. By 1899 (first report), *C. chemnitzia* was present in Tagus Cove, on Isabela Island (Table 1), however too little historical collection information is available to determine if *Caulerpa* was widespread and whether this report might represent an introduction. Named after the 1814 visit by an English war ship, the protected anchorage of Tagus Cove was historically popular with pirates and whalers, and was where Charles Darwin first landed on Isabela in 1835.

The reports and collections of *Caulerpa* presented here show its relatively cosmopolitan nature across oceanographic and marine biogeographic boundaries in the Galapagos (Edgar 2004; Palacios, 2004). However this distribution information is by no means geographically complete. Virtually all historical reports were from opportunistic sub-samplings of particular habitats (e.g. intertidal landing sites, protected lagoons, or monitoring sites) at specific locations. For example, Taylor (1945) collected *Caulerpa* only from the intertidal at Wolf Island's anchorage (far north of the archipelago), but did not sample other sites on the same island, or visit nearby Darwin Island during the expedition. A comprehensive investigation of the true *Caulerpa* distribution in the GMR is therefore necessary to create a more accurate and comprehensive baseline for quantifying future changes, and to identify appropriate monitoring locations.

*tuf*A barcoding of Galapagos specimens identified *C. chemnitzia* and *C. racemosa* locally. These findings are congruent with several of the historical epithets attributed in the Galapagos to these species (at the varietal or species level, Table 1) elsewhere (e.g. *C. peltata* has often been given to ecads of *C. chemnitzia*, see Belton et al. 2014). These results are also congruent biogeographically with recent sequencing efforts realized in the Tropical Eastern Pacific that documented these two species (Fernández et al. 2016). While these authors also reported the presence of *C. chemnitzia* in the Galapagos and *C.*

racemosa from the mainland coast of Ecuador, they did not sequence material from this location. Thus, we present the first confirmed record of these species in the Galapagos with molecular tools.

Of particular concern would be the introduction of *C. cylindraceae* (lineage F *sensu* Sauvage, et al 2013) into the GMR. *C. cylindraceae*, which originates from the southern Indian Ocean, has a relatively restricted native distribution along the Southwest shore of Western Australia (Verlaque et al., 2003, as *C. racemosa*), where it grows in intertidal pools and reef flats down to about 6m in depth, a common habitat type in the GMR. It has aggressively colonized both hard and soft substrates where it was introduced (Klein & Verlaque, 2008). Phenotypic plasticity in *C. chemnitzia* could potentially cause confusion in identification and mask new introductions of alien lineages. Therefore careful observations and measurements of new collections in combination with continued barcoding are of great importance.

Ecological and economic significance of *Caulerpa* in the GMR:

Island ecosystems are particularly susceptible to invasions (Denslow, 2003). Due to their ability to monopolize space and alter food webs, macroalgae are particularly damaging as marine invasive species (Schaffelke et al., 2006). Phase shifts from coral to macroalgal dominance on shallow tropical reefs have become commonplace (Fung et al., 2011) and climate change is predicted to intensify that process (Hoegh-Guldberg et al. 2007). Opportunistic macroalgal species tend to thrive following disturbance, and *Caulerpa* is a proven competitive dominant in both healthy and degraded systems. Therefore future predictions of *Caulerpa's* ecological role in the GMR will depend on a combination of intrinsic ecological and extrinsic environmental factors.

Variability in ocean temperatures and chemistry can influence coral-algal dynamics. Recent strong ENSO cycles and resulting sea surface temperature anomalies have resulted in widespread coral bleaching and mortality, and long-term changes in benthic community structure in the Tropical East Pacific (Glynn, 1988). ENSO cycles in the Eastern Tropical Pacific drive a dieback-regrowth pattern of invasive *Caulerpa* on Panamanian coral reefs: *Caulerpa* dies off during El Niño, but can find spatial refuge and survive until the subsequent La Niña period, when surviving patches of *Caulerpa* rapidly and completely overgrow reefs and kill corals (Smith et al., 2010).

Forecasts of future ENSO activity vary. However, corals in the GMR never fully recovered from the '82-83 event. Future ENSO-driven SST variation will undoubtedly further stress corals in the GMR, and limit their ability to compete for space. In terms of ocean chemistry, increasing atmospheric pCO_2 and subsequent oceanic absorption and acidification (Doney et al., 2009) has been shown to limit calcification of coral and urchin species (Fine & Tchernov, 2007; Asnaghi et al., 2013), while actually facilitating growth of invasive algal species like *Caulerpa* (Hall-Spencer & Allen, 2015). Cumulatively, these changes in sea surface temperature and chemistry could therefore

expedite further loss of corals. *C. chemnitzia* shares many life history and behaviour characteristics with the "killer algae" *C. taxifolia* (Klein & Verlaque, 2008), and here it is also important to note that published coral-*Caulerpa* interactions are particularly negative for prostrate, unbranched coral species, the most common growth form in Galapagos (Glynn & Wellington, 1983).

Introductions and subsequent invasions by *Caulerpa* can contribute to the decline of coral reefs and prevent recovery. Given the susceptibility of corals in the GMR to future perturbations in temperature (ENSO) and ocean chemistry, *Caulerpa's* potential to proliferate should be of concern to managers. Further loss of corals would mean overall loss of biodiversity in the GMR, and fundamental changes in ecosystem structure as coral-associated species are displaced. Other sessile marine life is also at risk, including sponges, tunicates, anemones, gorgonians, and non-dominant macroalgae, representative species of which may be unique to Galapagos.

True coral "reefs" in Galapagos are almost exclusively restricted to the far-North islands of Darwin and Wolf (Glynn & Wellington, 1983). There, *Caulerpa* has the potential to wreak the most economic havoc considering that the northern islands are a renowned ecotourism destination for divers, who pay premiums for live-aboard expeditions. While abundant marine megafauna (sharks, rays, dolphins, turtles) are the primary draw, the overall ecotourism experience would not be complete without healthy, abundant corals and their associated communities. In the last decades, tourist satisfaction with Galapagos nature and wildlife has declined due to crowding and development (Epler, 2007), and algae-covered coral reefs would undoubtedly further degrade their experience.

MANAGEMENT RECOMMENDATIONS

Without the ability to understand, predict, and directly measure the impacts of introduced seaweeds, the management of potentially invasive marine species in Galapagos needs to remain focused on early detection, rapid response, and control to reduce the likelihood of negative ecological impacts (Keith et al. 2016). Monitoring and management of *Caulerpa* should be made a high conservation priority in the GMR, and the following approaches are recommended.

1) Initial archipelago-wide surveys to establish an accurate and current baseline distribution of *Caulerpa* in the GMR, and identify sites of new colonizations where it was not previously reported. These should include both intertidal and subtidal (0-20 m) surveys, focusing on areas not normally sampled by current ecological monitoring efforts.

2) Permanent transects at established colonies and high-risk locations. Using the methods described above (photoquadrats) would allow for time-series analysis of changes in *Caulerpa* behaviour. Recommended monitoring sites include high traffic locations like Puerto Ayora (Academy Bay), Tortuga Bay, Puerto Baquerizo Moreno, Puerto Villamil, and Darwin Island (where a fixed monitoring transect is now in place).
3) Continued barcoding of extant *Caulerpa* populations in Galapagos with multiple DNA markers to provide a baseline of genetic diversity across the GMR. Sequencing of any newly identified populations is highly recommended to identify/record new introductions. Sequencing of mainland specimens would also be beneficial for comparison purposes, and genomic/transcriptomic efforts may be necessary to resolve the origin of the Galapagos strain although conservation efforts in the GMR should be prioritized.
4) Continued inspections of GMR-bound marine traffic (hulls and ballast water) both at mainland and Galapagos ports and identification of any discovered material. CDF and the marine invasive working group have conducted two capacity building and identification workshops for GNPD, ABG, NAVY and INOCAR technicians.
5) Conservation of *Chelonia mydas* and other important grazers. Stomach content analysis, anecdotal evidence, and direct observations have shown preferential grazing by *C. mydas*, the green sea turtle, on *Caulerpa* (Pritchard, 1971; Carrion-Cortez et al., 2010; pers. obs) in the GMR. These and other grazers (e.g. parrotfish, surgeonfish, chubs, large gastropods) could play a beneficial role in controlling the spread of *Caulerpa*, and should be given special conservation status.
6) Minimizing reef disturbance, particularly stresses associated with recreational diving and boating activities. High current in the GMR often results in divers and vessel anchors/chains physically interacting with reefs. Corals are easily broken, and *Caulerpa* can disperse via fragmentation. Tour operators should ensure that both their patrons and vessels minimize contact with reefs.
7) Utilizing the tourism sector. Diving, snorkelling, and intertidal walking tours have the potential to aid in monitoring the spread of *Caulerpa* in the GMR. These activities are ongoing and increasing throughout the archipelago, and dive tours frequently visit the Northern islands, which are otherwise costly and logistically difficult to monitor. In order to renew their licenses, all GNP naturalist guides participate in an actualisation course, during which *Caulerpa* identification has been taught in recent years. Here we stress the importance of GNP Naturalist Guides, tourists, and local community members continuing to report the presence of new species or changes in abundance and behaviours of species already

present, in order to improve the early detection and rapid response protocols that are in place.

In addition to the management recommendations outlined above, *Caulerpa* in Galapagos offers potential for further ecological and evolutionary studies. These include investigations of coral-*Caulerpa*-herbivore interactions, archipelago and regional-scale phylogenetics, influence of environment on morphology, etc. However, creating baselines of distributions and cover, and monitoring behaviour should be priorities. It is not yet known if this species will benefit from climate variability and recent changes in benthic community structure in Galapagos, which is why *Caulerpa* is a species of concern and a focus of future research in the GMR.

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General Discussion

The literature review offered many insights into the historical ecology of macroalgae in the Galapagos archipelago, while creating a foundation for future investigations to fill gaps in knowledge. Clearly, there are interesting patterns in macroalgal distributions and dynamics across regions and depths, and long-term changes may be driven by ENSO related processes. The abundance and diversity of macroalgal grazers in the system, whose existence is tightly linked to macroalgal productivity, highlights the trophic importance of macroalge in the coastal food webs of the Galapagos.

The large-scale survey effort showed that the functional compositions, biomasses, and production values of MaCs in Galapagos vary across sites and depths, and that MaC production is highly dependent on both overall cover and functional composition. Finer-scale resolution of macroalgal energy flows requires incorporation of this variation into macroalgal functional group parameterization. Previously, energy flow models for Galapagos sub-systems pooled all macroalgae into one functional group. Optimally, the functional group scheme (9 groups) and associated parameters presented in this work could be used to more clearly elucidate the role macroalge plays in structuring nearshore food webs across the Galapagos archipelago.

The investigation into the history, phylogenetics, and behavior of *Caulerpa* in the GMR contributed much to our knowledge of this potentially invasive taxa. Clearly, *Caulerpa* has the potential to further disturb and threaten the already-stressed coral reefs of the GMR. Ever-increasing human activity (specifically marine traffic) across the Galapagos means increasing risks of ecological invasions, and continued surveys and sampling combined with increasing vigilance across stakeholder groups is necessary to identify and mitigate new introductions and destructive behavioral changes in *Caulerpa* populations in the Galapagos marine ecosystem.

The Galapagos archipelago offers many opportunities for further studies of macroalgal ecology. Given that changes in net primary productivity can affect energy flow patterns in ecosystems, understanding macroalgal responses to fluctuating environmental factors will greatly enhance our ability to predict future changes in the structure and functionality of nearshore trophic webs in the Galapagos. This work provides the basis for mechanistic studies to identify the factors driving patterns in MaC community compositions. The future influence of continued increases in anthropogenic emissions, and subsequent changing climate, for example, may have great effects on macroalgal ecology, and offers an important avenue for future research.

Currently, the planet is experiencing relatively rapid atmospheric and oceanographic changes, which are affecting biogeochemical and ecological cycles. As we understand them, ENSO events are part of natural earth cycles, and such environmental changes have been shaping life on the planet since its inception. However, recent increases in human populations and subsequent resource exploitation are causing major changes to our earth system, with profound ecological consequences. It has been estimated that industrial and agricultural activities have increased atmospheric CO_2 concentrations about 100ppm over the last 250 years, resulting in faster rates of oceanic absorbance of carbon dioxide, and subsequent ocean acification (Doney et al., 2009). This

Experiments have shown deleterious effects of acidification on growth, reproduction, and survivorship of a range of calcifying marine organisms (Kroeker et al., 2010). Because of their ecological and biogeochemical importance, calcifying macroalgae, specifically coralline algae (Rhodophyta, Corallinales), have been extensively studied in terms of acidification effects. As they grow coralline algae precipitate high-magnesium calcite (one of the most soluble forms of bio-mineralized calcite), making corallines particularly sensitive to acidification. Generally, as pH is experimentally decreased, coralline algae show measurable declines in growth rate, reproductive potential, micro-structural integrity, and competitive capabilities (overgrowth by filamentous or fleshy macroalgal species; Andersson et al., 2008; Ries et al., 2009; Hofmann et al., 2011; Diaz-Pulido et al., 2012). In extremely low pH treatments, CCA simply dissolves (Büdenbender et al., 2011).

Other macroalgal functional groups on the other hand, have shown more variable responses, mostly due to their use of carbon-concentrating mechanisms (CCMs) to aid influx of carbon dioxide during limiting conditions (Raven, 1997). CCMs are metabolically expensive to produce, but become unnecessary and are actively suppressed as pCO2 increases (Giordano et al., 2005). Results of recent experiments testing the viability of CCM macrophytes in acidified waters indicate a generally positive relationship between physiology and pCO2, and these results could have profound ecological implications for macroalgal ecology in the Galapagos archipelago as atmospheric carbon dioxide continues to increase.

Calcareous macroalgae, specifically crustose coralline algae (CCA), is a common and important constituent of the macroalgal community of Galapagos, though their future in a high-CO2 world is in question. It has been speculated that a combination of CCA growth inhibition and possible increased metabolism of fleshy competitors will create a competitive shift toward more ephemeral filamentous and fleshy algal species on rocky reefs (Hepburn et al., 2011). Studies have shown that warming ocean temperatures may only exacerbate this process (Diaz-Pulido et al., 2012). Ultimately, the potential extent of ecological consequences stemming from ocean acidification in the Galapagos have yet to be empirically investigated, and offer an important and pressing research venture.

Despite potential effects on populations of associated species like the iconic marine iguana, long-term variability in macroalgal communities has yet to be comprehensively studied in the Galapagos. It is known anecdotally that past ENSO events have caused large-scale shifts in community compositions and eliminated once-dominant macroalgal species from the archipelago, but predictions of larger-scale effects of both short and long-term climactic and oceanographic variability on most species, and more importantly entire macroalgal communities, remain speculative at best. No efforts have yet been made to comprehensively describe historical trends in the spatio-temporal distribution of macroalgae in the archipelago, though this would be possible through analysis of the CDF's long-term ecological monitoring data.

While creating a baseline for macroalgal biogeographic patterns in the archipelago is of great importance, the ability to predict the effects of future anticipated changes in oceanography and climate on the marine ecosystems of the Galapagos archipelago would be well served by continuing large-scale studies of macroalgal dynamics. To create a holistic knowledge base of macroalgal ecology in the GMR, these studies should be coupled with experimentally-based investigations into the mechanisms which ultimately shape macroalgal ecological patterns. This information could then be used to more accurately predict the influence of either future strong ENSO events or ocean acidification on macroalgal distributions, community compositions, production, and energy flows in the Galapagos.

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APPENDIX

Appendix I – Supplements for Chapter 1

List of fish potentially grazing on macroalgae in Galapagos. This list was generated by cross-referencing the Charles Darwin Foundation Datazone's fish checklist, (http://www.darwinfoundation.org/datazone/checklists/vertebrates/pisces/) with dietary information found in fishbase (http://fishbase.sinica.edu.tw/search.php).
H = herbivore; O = omnivore; P = planktivore.

Genus	Species	Common name (English)	Family	Herbivore/ Omnivore
Prionurus	*laticlavius*	Razor surgeonfish	Acanthuridae	H
Acanthurus	*nigricans*	Velvet surgeonfish	Acanthuridae	H
Acanthurus	*triostegus*	Convict surgeon	Acanthuridae	H
Acanthurus	*xanthopterus*	Ringtailed surgeonfish	Acanthuridae	H/O
Naso	*brevirostris*	Spotted unicornfish	Acanthuridae	H
Naso	*vlamingii*	Bignose unicornfish	Acanthuridae	O
Microspathodon	*dorsalis*	Giant damselfish	Pomacentridae	H
Microspathodon	*bairdii*	Bumphead damselfish	Pomacentridae	H
Stegastes	*beebei*	Southern whitetail major	Pomacentridae	H
Stegastes	*arcifons*	Island major	Pomacentridae	H
Stegastes	*acapulcoensis*	Acapulco major	Pomacentridae	H
Abudefduf	*troschelii*	Seargent major	Pomacentridae	H/P
Nexilosus	*latifrons*	Coquito sergeant	Pomacentridae	H
Abudefduf	*concolor*	Dusky seargent	Pomacentridae	H/P
Holocanthus	*passer*	King angelfish	Pomacanthidae	H/O
Girella	*freminvilli*	Dusky chub	Kyphosidae	H
Kyphosus	*analogus*	Blue-bronze sea chub	Kyphosidae	H
Kyphosus	*elegans*	Cortez sea chub	Kyphosidae	H
Chaetodon	*auriga*	Threadfin butterflyfish	Chaetodontidae	O
Chaetodon	*humeralis*	Threebanded butterflyfish	Chaetodontidae	O
Chaetodon	*kleinii*	Sunburst butterflyfish	Chaetodontidae	O
Chaetodon	*lunula*	Raccoon butterflyfish	Chaetodontidae	O
Johnrandallia	*nigrirostris*	Blacknosed butterflyfish	Chaetodontidae	O
Prognathodes	*carlhubbsi*	Southern scythe-marked butterflyfish	Chaetodontidae	O
Eucinostomus	*argenteus*	Silver mojarra	Chaetodontidae	O
Eucinostomus	*currani*	Pacific flagfin mojarra	Chaetodontidae	O
Eucinostomus	*dowii*	Dow's mojarra	Gerreidae	O

Genus	Species	Common name (English)	Family	Herbivore/ Omnivore
Bodianus	*eclancheri*	Galapagos hogfish	Labridae	O
Calotomus	*carolinus*	Carolines parrotfish	Scaridae	H
Nicholsina	*denticulata*	Loosetooth parrotfish	Scaridae	H
Scarus	*compressus*	Azure parrotfish	Scaridae	H
Scarus	*ghobban*	Blue-barred parrotfish	Scaridae	H
Scarus	*perrico*	Bumphead parrotfish	Scaridae	H
Scarus	*rubroviolaceus*	Ember parrotfish	Scaridae	H
Ophioblennius	*steindachneri*	Large-banded blenny	Blenniidae	H/O
Oplegnathus	*insignis*	Pacific beakfish	Oplegnathidae	H/O
Athron	*hispidus*	White-spotted puffer	Tetraodontidae	O
Canthigaster	*amboinensis*	Sharpnose pufferfish	Tetraodontidae	H/O
Melichthys	*niger*	Black triggerfish	Balistidae	H/O
Melichthys	*vidua*	Pink triggerfish	Balistidae	H/O
Aluterus	*scriptus*	Scribbled leatherjacket filefish	Monacanthidae	O
Cantherhines	*dumerilii*	Whitespotted filefish	Monacanthidae	O
Ostracion	*meleagris*	Whitespotted boxfish	Ostraciidae	O
Chanos	*chanos*	Milkfish	Chanidae	O

Appendix II – Supplements for Chapter 2

RHODOPHYTA			
Family	**Genus**	**Species**	**Group**
Erythrotrichiace	Erythrotrichia	carnea	2
Erythrotrichiace	Erythrotrichia	polymorpha	2
Erythrotrichiace	Erythrotrichia	reflexa	2
Acrochaetiaceae	Acrochaetium	microscopicum	2
Ceramiaceae	Gymnothamnion	elegans	2
Ceramiaceae	Centroceras	clavulatum	2
Ceramiaceae	Centroceras	fimbriatum	2
Ceramiaceae	Centroceras	gasparrinii	2
Ceramiaceae	Ceramium	affine	2
Ceramiaceae	Ceramium	cimbricum	2
Ceramiaceae	Ceramium	clarionense	2
Ceramiaceae	Ceramium	fimbriatum	2
Ceramiaceae	Ceramium	hoodii	2
Ceramiaceae	Ceramium	horridum	2
Ceramiaceae	Ceramium	howellii	2
Ceramiaceae	Ceramium	macilentum	2
Ceramiaceae	Ceramium	prostratum	2
Ceramiaceae	Ceramium	recticorticum	2
Ceramiaceae	Ceramium	serpens	2
Ceramiaceae	Ceramium	templetonii	2
Dasyaceae	Dasya	baillouviana	2
Dasyaceae	Heterosiphonia	crispella	2
Dasyaceae	Heterosiphonia	erecta	2
Dasyaceae	Heterosiphonia	subdisticha	2
Rhodomelaceae	Alsidium	pusillum	2
Rhodomelaceae	Neosiphonia	howei	2
Rhodomelaceae	Neosiphonia	simplex	2
Rhodomelaceae	Osmundea	sinicola	2
Rhodomelaceae	Bostrychia	calliptera	2
Rhodomelaceae	Bostrychia	radicans	2
Rhodomelaceae	Bostrychia	simpliciuscula	2
Rhodomelaceae	Bostrychia	tenella	2
Rhodomelaceae	Herposiphonia	secunda	2
Rhodomelaceae	Polysiphonia	bifurcata	2
Rhodomelaceae	Polysiphonia	decussata	2
Rhodomelaceae	Polysiphonia	scopulorum	2

Family	Genus	Species	Group
Rhodomelaceae	Polysiphonia	sertularioides	2
Rhodomelaceae	Pterosiphonia	dendroidea	2
Rhodomelaceae	Pterosiphonia	paucicorticata	2
Wrangeliaceae	Anotrichium	tenue	2
Wrangeliaceae	Griffithsia	pacifica	2
Wrangeliaceae	Tiffaniella	phycophilum	2
Wrangeliaceae	Tiffaniella	snyderae	2
Wrangeliaceae	Pleonosporium	complanatum	2
Colaconemataceae	Colaconema	daviesii	2
Delesseriaceae	Austrofolium	equatorianum	3
Delesseriaceae	Austrofolium	howellii	3
Delesseriaceae	Phycodrina	elegans	3
Delesseriaceae	Pseudolaingia	hancockii	3
Delesseriaceae	Taenioma	perpusillum	3
Delesseriaceae	Caloglossa	leprieurii	3
Delesseriaceae	Hypoglossum	attenuatum	3
Delesseriaceae	Nitophyllum	divaricatum	3
Delesseriaceae	Nitophyllum	galapagense	3
Delesseriaceae	Acrosorium	fragile	3
Delesseriaceae	Acrosorium	papenfussii	3
Delesseriaceae	Cryptopleura	crispa	3
Delesseriaceae	Cryptopleura	imbricata	3
Delesseriaceae	Cryptopleura	ruprechtiana	3
Delesseriaceae	Cryptopleura	violacea	3
Delesseriaceae	Myriogramme	kylinii	3
Rhodomelaceae	Herposiphonia	secunda	3
Halymeniaceae	Cryptonemia	limensis	3
Halymeniaceae	Halymenia	santamariae	3
Scinaiaceae	Scinaia	latifrons	3
Schizymeniaceae	Schizymenia	ecuadoreana	3
Rhodomeniales	Sciadophycus	stellatus	3
Rhodomelaceae	Herposiphonia	subdisticha	4
Dumontiaceae	Dilsea	sp.	4
Gigartinaceae	Chondrus	albemarlensis	4
Gigartinaceae	Iridaea	sp.	4
Kallymeniaceae	Callophyllis	ligulata	4
Kallymeniaceae	Kallymenia	multiloba	4
Kallymeniaceae	Kallymenia	setchellii	4
Kallymeniaceae	Pugetia	latiloba	4
Gracilariaceae	Gracilaria	skottsbergii	4

Family	Genus	Species	Group
Gracilariaceae	Gracilaria	textorii	4
Faucheaceae	Fauchea	galapagensis	4
Faucheaceae	Gloiocladia	galapagensis	4
Rhodymeniaceae	Halichrysis	irregularis	4
Ahnfeltiaceae	Ahnfeltia	durvillei	5
Ahnfeltiaceae	Ahnfeltia	svensonii	5
Bonnemaisoniaceae	Asparagopsis	sanfordiana	5
Bonnemaisoniaceae	Asparagopsis	taxiformis	5
Callithamniaceae	Callithamnion	ecuadoreanum	5
Callithamniaceae	Callithamnion	epiphyticum	5
Callithamniaceae	Callithamnion	rupicola	5
Ceramiaceae	Ardreanema	seriospora	5
Ceramiaceae	Antithamnion	veleroae	5
Ceramiaceae	Gayliella	flaccida	5
Ceramiaceae	Antithamnionella	breviramosa	5
Ceramiaceae	Platythamnion	reversum	5
Ceramiaceae	Scagelia	pylaisaei	5
Rhodomelaceae	Chondria	acrorhizophora	5
Rhodomelaceae	Chondria	flexicaulis	5
Rhodomelaceae	Laurencia	mediocris	5
Rhodomelaceae	Laurencia	obtusa	5
Rhodomelaceae	Laurencia	oppositocladia	5
Gelidiaceae	Gelidium	crinale	5
Gelidiaceae	Gelidium	filicinum	5
Gelidiaceae	Gelidium	galapagense	5
Gelidiaceae	Gelidium	hancockii	5
Gelidiaceae	Gelidium	isabelae	5
Gelidiaceae	Gelidium	pusillum	5
Gelidiaceae	Gelidium	pusillum	5
Gelidiaceae	Gelidium	sclerophyllum	5
Gelidiaceae	Gelidium	serrulatum	5
Gelidiaceae	Pterocladiella	capillacea	5
Gelidiellaceae	Gelidiella	machrisiana	5
Gelidiellaceae	Parviphycus	tenuissimus	5
Areschougiaceae	Agardhiella	subulata	5
Areschougiaceae	Sarcodiotheca	divaricata	5
Areschougiaceae	Sarcodiotheca	ecuadoreana	5
Areschougiaceae	Sarcodiotheca	furcata	5
Areschougiaceae	Sarcodiotheca	gaudichaudii	5
Areschougiaceae	Sarcodiotheca	tenuis	5

Family	Genus	Species	Group
Caulacanthaceae	Catenella	caespitosa	5
Cystocloniaceae	Hypnea	pannosa	5
Cystocloniaceae	Hypnea	spinella	5
Cystocloniaceae	Hypnea	valentiae	5
Dumontiaceae	Leptocladia	binghamiae	5
Dumontiaceae	Leptocladia	laxa	5
Gigartinaceae	Chondracanthus	acicularis	5
Gigartinaceae	Chondracanthus	tepidus	5
Phyllophoraceae	Ahnfeltiopsis	durvillei	5
Phyllophoraceae	Ahnfeltiopsis	smithii	5
Phyllophoraceae	Gymnogongrus	griffithsiae	5
Phyllophoraceae	Stenogramma	interrupta	5
Rhizophyllidaceae	Ochtodes	crockeri	5
Rhizophyllidaceae	Ochtodes	secundiramea	5
Gracilariaceae	Gracilaria	ecuadoreanus	5
Gracilariaceae	Gracilariopsis	panamensis	5
Halymeniaceae	Carpopeltis	bushiae	5
Halymeniaceae	Grateloupia	howei	5
Halymeniaceae	Grateloupia	versicolor	5
Halymeniaceae	Prionitis	abbreviata	5
Halymeniaceae	Prionitis	acroidalea	5
Halymeniaceae	Prionitis	albemarlensis	5
Halymeniaceae	Prionitis	galapagensis	5
Halymeniaceae	Prionitis	hancockii	5
Galaxauraceae	Dichotomaria	marginata	5
Galaxauraceae	Dichotomaria	obtusata	5
Galaxauraceae	Dichotomaria	spathulata	5
Galaxauraceae	Galaxaura	barbata	5
Galaxauraceae	Galaxaura	filamentosa	5
Galaxauraceae	Galaxaura	intermedia	5
Galaxauraceae	Galaxaura	marginata	5
Scinaiaceae	Scinaia	complanata	5
Scinaiaceae	Scinaia	johnstoniae	5
Scinaiaceae	Scinaia	setchellii	5
Plocamiaceae	Plocamium	cartilagineum	5
Plocamiaceae	Plocamium	cartilagineum	5
Champiaceae	Champia	parvula	5
Lomentariaceae	Gelidiopsis	intricata	5
Lomentariaceae	Gelidiopsis	variabilis	5
Rhodymeniaceae	Botryocladia	pseudodichotoma	5

Family	Genus	Species	Group
Rhodymeniaceae	Botryocladia	tenuissima	5
Rhodymeniaceae	Rhodymenia	californica	5
Rhodymeniaceae	Rhodymenia	dawsonii	5
Rhodymeniaceae	Rhodymenia	decumbens	5
Rhodymeniaceae	Rhodymenia	divaricata	5
Rhodymeniaceae	Rhodymenia	flabellifolia	5
Palmariaceae	Palmaria	palmata	6
Corallinaceae	Amphiroa	beauvoisii	7
Corallinaceae	Amphiroa	compressa	7
Corallinaceae	Amphiroa	crustiformis	7
Corallinaceae	Amphiroa	dimorpha	7
Corallinaceae	Amphiroa	galapagensis	7
Corallinaceae	Amphiroa	peruana	7
Corallinaceae	Amphiroa	polymorpha	7
Corallinaceae	Amphiroa	rigida	7
Corallinaceae	Amphiroa	valonioides	7
Corallinaceae	Amphiroa	vanbosseae	7
Corallinaceae	cf. Corallina	berterii	7
Corallinaceae	Corallina	officinalis	7
Corallinaceae	Corallina	officinalis	7
Corallinaceae	Corallina	pinnatifolia	7
Corallinaceae	Corallina	vancouveriensis	7
Corallinaceae	Jania	capillacea	7
Corallinaceae	Jania	ungulata	7
Sporolithaceae	Archaeolithothamnion	crosslandii	8
Sporolithaceae	Archaeolithothamnion	pacificum	8
Sporolithaceae	Pseudolithophyllum	decipiens	8
Corallinaceae	Lithophyllum	alternans	8
Corallinaceae	Lithophyllum	amplostratum	8
Corallinaceae	Lithophyllum	claudescens	8
Corallinaceae	Lithophyllum	complexum	8
Corallinaceae	Lithophyllum	decussatum	8
Corallinaceae	Lithophyllum	divaricatum	8
Corallinaceae	Lithophyllum	duckerae	8
Corallinaceae	Lithophyllum	frutescens	8
Corallinaceae	Lithophyllum	intermedium	8
Corallinaceae	Lithophyllum	moluccense	8
Corallinaceae	Lithophyllum	mutabile	8
Corallinaceae	Lithophyllum	prototypum	8
Corallinaceae	Lithophyllum	rileyi	8

Family	Genus	Species	Group
Corallinaceae	Lithophyllum	sancti-georgei	8
Corallinaceae	Lithophyllum	veleroae	8
Corallinaceae	Titanoderma	erecta	8
Corallinaceae	Titanoderma	pustulatum	8
Corallinaceae	Hydrolithon	onkodes	8
Corallinaceae	Hydrolithon	samo•nse	8
Corallinaceae	Neogoniolithon	brassica-florida	8
Corallinaceae	Neogoniolithon	frutescens	8
Corallinaceae	Neogoniolithon	trichotomum	8
Corallinaceae	Spongites	decipiens	8
Hapalidiaceae	Choreonema	thuretii	8
Hapalidiaceae	Lithothamnion	cottoni	8
Hapalidiaceae	Lithothamnion	fragiissimum	8
Hapalidiaceae	Lithothamnion	phymatodeum	8
Hapalidiaceae	Lithothamnion	pocillum	8
Hapalidiaceae	Melobesia	accola	8
Hapalidiaceae	Melobesia	galapagensis	8
Hapalidiaceae	Melobesia	marginata	8
Hapalidiaceae	Melobesia	membranacea	8
Hapalidiaceae	Mesophyllum	laxum	8
Hildenbrandiaceae	Hildenbrandia	galapagensis	9
Hildenbrandiaceae	Hildenbrandia	occidentalis	9
Hildenbrandiaceae	Hildenbrandia	rubra	9
Peyssonneliaceae	Peyssonnelia	clarionensis	9
Peyssonneliaceae	Peyssonnelia	dubyi	9
Peyssonneliaceae	Peyssonnelia	mexicana	9
Peyssonneliaceae	Peyssonnelia	rubra	9

OCHROPHYTA			
Family	**Genus**	**Species**	**Group**
Desmarestiaceae	Desmarestia	ligulata	6
Desmarestiaceae	Desmarestia	munda	6
Desmarestiaceae	Desmarestia	tropica	6
Dictyotaceae	Dictyota	binghamiae	3
Dictyotaceae	Dictyota	dichotoma	3
Dictyotaceae	Dictyota	dichotoma	3
Dictyotaceae	Dictyota	flabellata	3
Dictyotaceae	Dictyota	galapagensis	3
Dictyotaceae	Dictyota	major	3
Dictyotaceae	Dictyopteris	cokeri	3
Dictyotaceae	Dictyopteris	diaphana	3
Dictyotaceae	Lobophora	variegata	9
Dictyotaceae	Padina	concrescens	4
Dictyotaceae	Padina	crispata	4
Dictyotaceae	Padina	durvillaei	4
Dictyotaceae	Spatoglossum	howellii	6
Dictyotaceae	Spatoglossum	schmittii	6
Dictyotaceae	Spatoglossum	schroederi	6
Dictyotaceae	Spatoglossum	sp. 1	6
Dictyotaceae	Taonia	lennebackerae	3
Chordariaceae	Spongonema	tomentosum	5
Chordariaceae	Zosterocarpus	abyssicolus	2
Ectocarpaceae	Pilinia	maritima	2
Mesosporaceae	Mesospora	pangoensis	9
Sargassaceae	Bifurcaria	galapagensis	5
Sargassaceae	Sargassum	albermarlense	5
Sargassaceae	Sargassum	brandegeei	5
Sargassaceae	Sargassum	cymosum	5
Sargassaceae	Sargassum	galapagense	5
Sargassaceae	Sargassum	galapagense	5
Sargassaceae	Sargassum	howellii	5
Sargassaceae	Sargassum	ilicifolium	5
Sargassaceae	Sargassum	lendigerum	5
Sargassaceae	Sargassum	obtusifolium	5
Sargassaceae	Sargassum	pacificum	5
Sargassaceae	Sargassum	pacificum	5
Sargassaceae	Sargassum	pacificum	5
Sargassaceae	Sargassum	pacificum	5
Sargassaceae	Sargassum	pacificum	5

Family	Genus	Species	Group
Sargassaceae	Sargassum	setifolium	5
Sargassaceae	Sargassum	templetonii	5
Sargassaceae	Sargassum	zacae	5
Lessoniaceae	Eisenia	galapagensis	6
Chnoosporaceae	Chnoospora	implexa	5
Scytosiphonaceae	Colpomenia	bullosa	4
Scytosiphonaceae	Colpomenia	ramosa	4
Scytosiphonaceae	Colpomenia	sinuosa	4
Scytosiphonaceae	Colpomenia	tuberculata	4
Scytosiphonaceae	Petalonia	sp.	4
Sphacelariaceae	Sphacelaria	novae-hollandiae	2
Sphacelariaceae	Sphacelaria	rigidula	2
Sporochnaceae	Carpomitra	sp. 1	5
Sporochnaceae	Sporochnus	bolleanus	5
Sporochnaceae	Sporochnus	rostratus	5

CHLOROPHYTA			
Family	**Genus**	**Species**	**Group**
Bryopsidaceae	Bryopsidella	neglecta	2
Bryopsidaceae	Bryopsis	galapagensis	2
Bryopsidaceae	Bryopsis	hypnoides	2
Bryopsidaceae	Bryopsis	indica	2
Bryopsidaceae	Bryopsis	maxima	2
Bryopsidaceae	Bryopsis	pennata	2
Bryopsidaceae	Bryopsis	ramulosa	2
Caulerpaceae	Caulerpa	peltata	5
Caulerpaceae	Caulerpa	racemosa	5
Caulerpaceae	Caulerpa	racemosa	5
Caulerpaceae	Caulerpella	ambigua	5
Codiaceae	Boodleopsis	pusilla	2
Codiaceae	Codium	brandegeei	5/9
Codiaceae	Codium	dichotomum	5/9
Codiaceae	Codium	fernandezianum	5/9
Codiaceae	Codium	foveolatum	5/9
Codiaceae	Codium	isabelae	5/9
Codiaceae	Codium	setchellii	5/9
Derbesiaceae	Derbesia	hollenbergii	2
Derbesiaceae	Derbesia	marina	2
Derbesiaceae	Derbesia	prolifica	2
Udoteaceae	Chlorodesmis	hildebrandtii	2
Oedogoniaceae	Oedogonium	sp.	2
Chaetophoraceae	Zygomitus	reticulatus	2
Cladophoraceae	Chaetomorpha	antennina	2
Cladophoraceae	Chaetomorpha	brachygona	2
Cladophoraceae	Chaetomorpha	linum	2
Cladophoraceae	Cladophora	perpusilla	2
Cladophoraceae	Cladophora	prolifera	2
Cladophoraceae	Cladophora	sp.	2
Cladophoraceae	Rhizoclonium	crasspellitum	2
Cladophoraceae	Rhizoclonium	implexum	2
Cladophoraceae	Rhizoclonium	rhizophilum	2
Cladophoraceae	Rhizoclonium	riparium	2
Cladophoraceae	Rhizoclonium	robustum	2
Ulotrichaceae	Spongomorpha	conjuncta	2
Ulvaceae	Ulva	clathrata	3
Ulvaceae	Ulva	fasciata	3
Ulvaceae	Ulva	flexuosa	3

Family	Genus	Species	Group
Ulvaceae	Ulva	lactuca	3
Ulvaceae	Ulva	linza	3
Ulvaceae	Ulva	lobata	3
Ulvaceae	Ulva	prolifera	3
Ulvaceae	Ulva	taeniata	3
Ulvellaceae	Acrochaete	viridis	2
Ulvellaceae	Entocladia	thivyae	2
Ulvellaceae	Phaeophila	dendroides	2
Ulvellaceae	Ulvella	viridis	2

Galapagos Macroalgal species lists and functional groupings

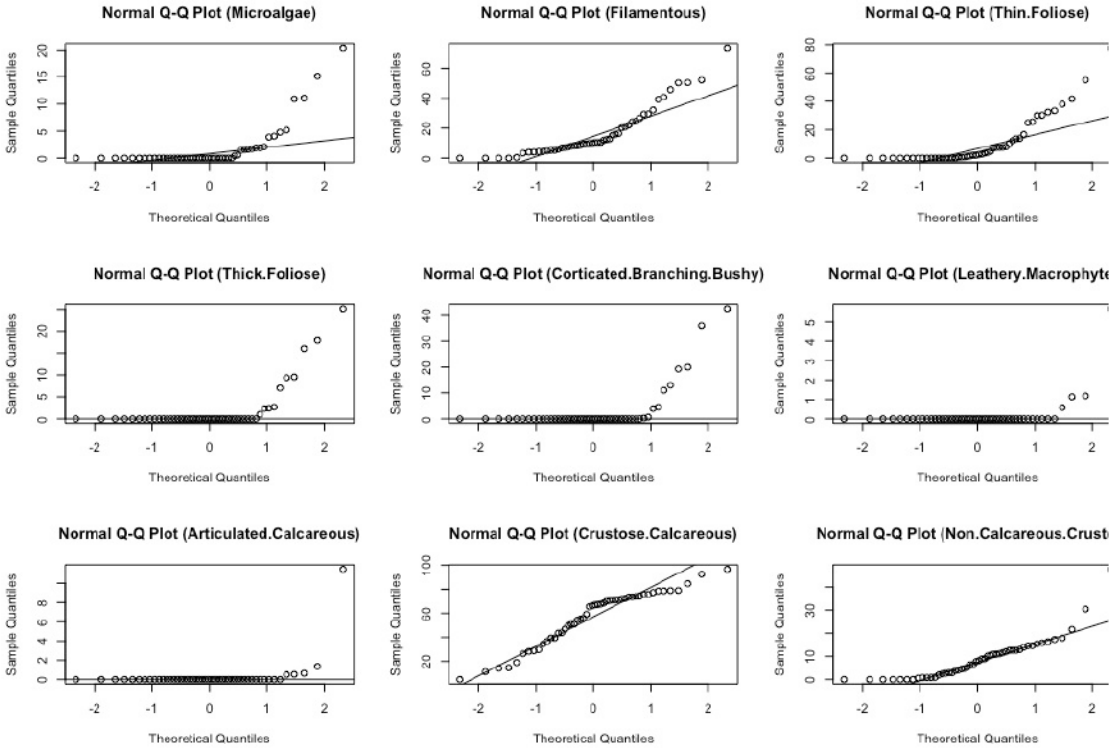
Table 2.1 Functional groups % Cover matrix

Transect	Microalgae	Filamentous	Thin Foliose	Thick Foliose	Corticated Branching Bushy	Leathery	Articulated Calcareous	Calcareous Crustose	Non-Calcareous Crustose
DA00(15)	0	5.3	7.6	1	0	0	1.36	70.13	14.61
DA01(15)	4.0486	39.2713	32.3887	0	0	0	0	11.3360	12.9555
DA01(6)	0.4577	8.6957	33.4096	0	0	0	0	43.48	13.9588
ES02(15)	10.9422	8.2067	0	0	3.9514	0	0	74.0122	2.8875
ES02(6)	0	20.88	0.68	0	0	0	0	70.63	8.15
ES03(15)	0	9.85	0	0	0	0	0	78.99	11.16
ES12(15)	0	5.96	10.39	0	0	0	0	71.02	12.63
ES12(6)	0	7.3113	25	0	0	0	0	49.7642	17.9245
FE01(15)	0	0	0	9.55	42.69	0	11.46	14.65	21.66
FE01(6)	0	22.03	30.02	2.34	36.06	0.58	0	4.87	4.09
FE03(15)	0	0	4	16	20	0	0	51	9
FE03(6)	0	8	55	7	11	0	0	19	0
FL04(15)	1.91	0.41	0	25.16	0	0	0	67.25	5.27
FL06(15)	0	52.1127	7.5117	0	0	0	0	39.4366	0.9390
FL06(6)	0	29.3310	13.8937	0	0	0	0	54.3739	2.4014
FL13(15)	0	40.6948	1.9851	0	0	0	0	50.8685	6.4516
FL13(6)	1.5666	45.69191	0	0	0	0	0	43.8642	8.8773

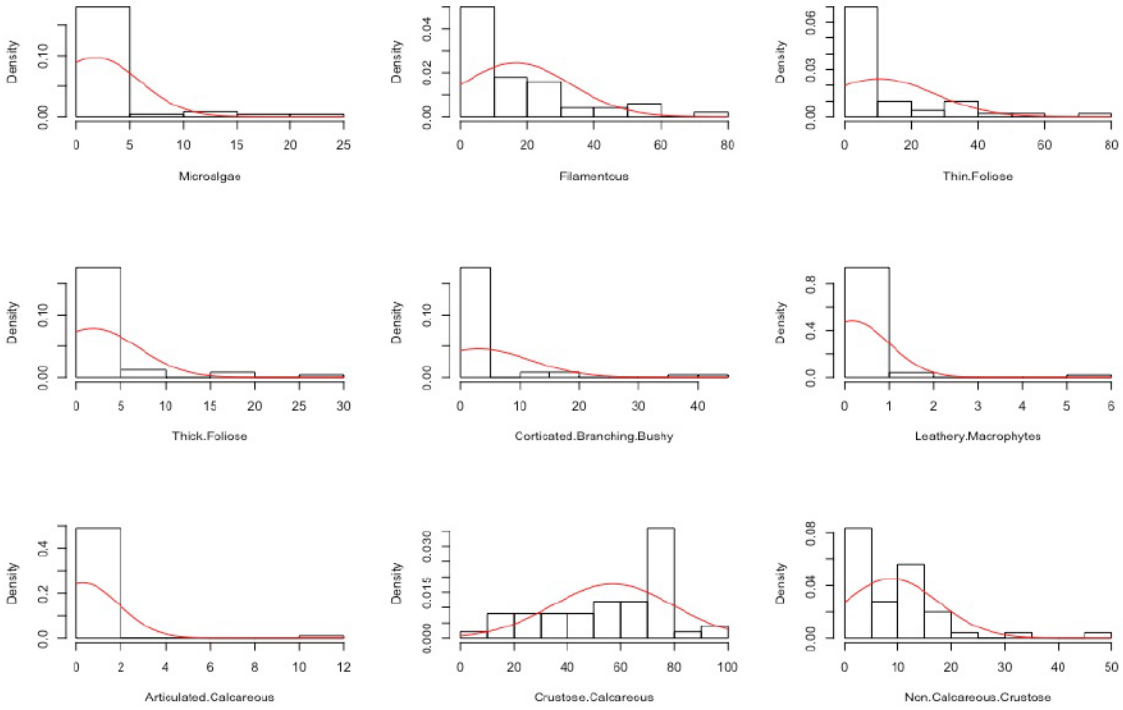
Transect	Microalgae	Filamentous	Thin Foliose	Thick Foliose	Corticated Branching Bushy	Leathery	Articulated Calcareous	Calcareous Crustose	Non-Calcareous Crustose
IS01(6)	0	24.71	0	0	0	0	0.64	71.97	2.68
IS24(15)	1.9	26.58	41.77	0	0	0	0	29.75	0
IS24(6)	0	6.86	77.71	0	0.63	0	0	14.23	0.57
IS41(15)	1.63	10.5	0.84	9.39	0.25	1.13	0	68.5	7.76
IS41(6)	3.88	10.48	12.29	17.85	4.52	5.69	0	34.41	10.88
IS42(15)	0	0	3.5235	2.6846	19.2953	1.1745	0	66.9463	6.3758
PI00(15)	0	16.4623	0	0	0	0	0	70.9282	12.6095
PI00(6)	0	12.4138	0	0	0	0	0	75.5172	12.0690
PI01(15)	1.7118	15.2639	0	0	0	0	0	67.6177	15.4066
PI01(6)	2.0833	15.9722	0	0	0	0	0	71.3889	10.5556
SB06(15)	0	4.41	0	2.42	0	0	0	78.52	14.65
SB09(15)	0	4.03	0	0	0	0	0	78.63	17.34
SB09(6)	5.19	12.82	37.99	0	0	0	0	39.45	4.55
SB10(15)	0	3.33	0	0	0	0	0	96.67	0
SB10(6)	0	5.25	16.69	0	0	0	0	77.28	0.78
SC07(15)	11.08	3.94	1.17	0	0	0	0	73.62	10.19
SC07(6)	0	0	7.49	0	0	0	0	92.51	0
SC08(6)	0	50.41	0	0	13.01	0	0	36.59	0
SC09(6)	0	73.64	0	0	0	0	0	26.36	0
SC10(15)	15.15	8.27	0	0	0	0	0	75.74	0.84
SC10(6)	20.38	7.07	7.07	0	0	0	0	65.49	0
SC11(15)	0	11.97	2.82	0	0	0	0	73.59	11.62
SC12(15)	0	10.45	0	0	0	0	0	59.1	30.45
SC12(6)	4.78	29.45	7.94	0	0	0	0	55.86	1.97
SC13(15)	0	20.29	2.54	0	0	0	0	72.39	4.78
SC14(15)	0	9.43	2.06	0	0	0	0	84.66	3.85

Transect	Microalgae	Filamentous	Thin Foliose	Thick Foliose	Corticated Branching Bushy	Leathery	Articulated Calcareous	Calcareous Crustose	Non-Calcareous Crustose
SC14(6)	0.58	4.84	25.53	0	0	0	0	66.15	2.9
SC15(15)	0	32.1	0	0	0	0	0	55.26	12.64
WO01(15)	0	9.848484848	13.63636364	0	0	0	0	28.7879	47.7272
WO01(6)	1.485148515	24.27	30.1980198	0	0	0	0	28.2178	15.8416
WO05(15)	0	9.5	0.6	0	0	0	0	78.9	11
WO05(6)	0	4.34	4.691689008	0	0	0	0.5	74.13	16.3539

Q-Q plots of univariate residuals (per functional group).



Histograms of univariate distributions (per functional group)



Eidesstattliche Versicherung

Erklärung

Hiermit erkläre ich, dass ich die Doktorarbeit mit dem Titel:

Historical knowledge, variation in community composition, ecotrophic parameterization, and invasive species of macroalgae in the Galapagos archipelago

selbstständig verfasst und geschrieben habe und außer den angegebenen Quellen keine weiteren Hilfsmittel verwendet habe.

Ebenfalls erkläre ich hiermit, dass es sich bei den von mir abgegebenen Arbeiten und drei identische Exemplare handelt.

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(Unterschrift)